AN ANALYSIS OF CERTAIN CASES OF INTRA-SPECIFIC STERILITY[1]

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	501
Fused	502
a. Sterility in the fused stock	502
b. Search for a factor for sterility	506
c. Production of but one sex by fused females	509
d. Discussion of peculiarities shown by fused	512
Rudimentary	513
a. The theories of prematuration and repugnance	513
b. Search for a factor for sterility	521
c. Additional mutations to rudimentary	522
Morula	524
Reduced bristle	526
Dibro	527
Dwarf	527
Cleft	528
GENERAL DISCUSSION	529
SUMMARY	532
LITERATURE CITED	533

INTRODUCTION

In the course of the experiments upon *Drosophila melanogaster* Meigen (*ampelophila* Loew) carried on at COLUMBIA UNIVERSITY, a number of mutant stocks have been obtained in which either the male or female produces few or no young. On account of both its economic and its scientific interest the general phenomenon of sterility has been the subject of investigation and discussion for a period of many years and the mass of facts which has accumulated has served to demonstrate the complexity of the problem. One of the principal conclusions from the evidence is, that the various phases of sterility are undoubtedly to be referred to diverse causes. It is a widespread belief that one of the commonest causes is the

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process of inbreeding and in several cases this idea has been supported by experimental evidence, but in the present instance, such a connection is not involved since in every race investigated the attribute in question appears in conjunction with specific somatic characters and follows the distribution of the mutant gene responsible for them, regardless of whether the stock has been inbred or not. In fact, on account of the sterility involved, out-crossing has usually been a necessity for the continuation of the strain. With the Mendelian theory as an instrument of investigation, it has been possible to demonstrate the existence of definite factors which are responsible for the degree of sterility shown. One such factor has already been indicated in Drosophila by the work of HYDE (1911) and two in the fowl by PEARL (1912). With the possibility of other similar discoveries in view, a brief inquiry into the nature and behavior of certain sterile stocks of Drosophila was begun.

The mutant races examined were seven in number and included rudimentary wings, fused wings, cleft wings, morula eyes, reduced bristle, dwarf body, and dibro. These characters are due to recessive genes widely distributed in the germ plasm, as the first three have been located in the first or X chromosome, morula and reduced bristle in the second, and dwarf in the third. Dibro has not yet been placed. In most of these strains it is the female which is markedly unproductive, but in cleft, however, the male is sterile, and since the character is sex-linked it has been impossible to obtain cleft females. In dibro both sexes have so far proved completely sterile, and a large enough number of individuals has not yet been tested to make it certain that fertile ones are not produced.

FUSED

a. *Sterility in the fused stock*

The gene representing fused has been located at 59.5 in the X chromosome. Its chief effect upon the soma is to produce a more or less complete fusion of the third and fourth wing veins and a striking degree of infertility in the female. Stock is kept up by mating the male with heterozygous females and thus obtaining normal males and normal females and fused males and fused females in practically a 1 : 1 : 1 : 1 ratio. Table 1 summarizes the results from ten such crosses. Two exceptional classes, eosin-eyed females and red males, due to non-disjunction, may be omitted and the eye colors, eosin, white and red, disregarded in the comparison of the fused and normal offspring. The total number of

TABLE 1

Normal ♀ heterozygous for fused by red fused ♂.

No. of culture	Normal ♀♀	Fused ♀♀	Eosin ♀♀	Eosin ♂♂	White ♂♂	Eosin fused ♂♂	White fused ♂♂	Red fused ♂♂	Total
L	95	76	13	43	34	31	30	6	328
K	94	56	6	42	37	16	30	8	289
B	108	123	14	71	35	54	69	7	481
F	110	76	8	52	28	36	55	8	373
D	95	122		56	29	31	76		409
A	87	82		45	29	32	43		318
H	102	121		52	38	54	49		416
2	47	39	4	29	17	20	30	1	187
3	53	45	10	32	18	17	25	3	203
4	53	46	4	38	23	20	43		227
	844	786	59	460	288	311	450	33	
Total	844	786		748		761			

flies per bottle is slightly below normal but this may be accounted for in part by the fact that the temperature was below the optimum and because no effort was made to continue the counts up to the very end of the hatching period, nor were the females transferred to fresh bottles of food in order to obtain the maximum output of eggs. However, even allowing for these circumstances, we are probably justified in concluding that the heterozygous female is slightly affected in the direction of sterility by the presence in her chromosomal constitution of the factor for fused. The totals obtained for the four classes are: normal females 844, fused females 786, normal males 748, fused males 761. It is a general rule in any cross in Drosophila that fewer males than females are produced unless counts are continued until the bottle runs out so that the slight differences in regard to the sexes observed here may not be of particular significance. Comparing the total number of normal individuals with the total number of fused (exclusive of the two exceptional classes) we find there are 1592 to 1547,—figures which do not suggest any noticeable difficulty in the formation of the fused class from the heterozygous type. The harmfulness of the fused gene, therefore, affects the entire output of gametes in the heterozygous female rather than any one variety.

The low fertility of the fused female seems to be partly due to the fact that the normal number of eggs is not produced. Examination of the ovaries shows that fewer eggs than usual mature and by means of

egg counts it was ascertained that the number laid is below normal. Table 2 gives the data from seven crosses showing the number of eggs laid and of flies hatched therefrom. The largest number of eggs deposited by any one female was 88, none of which produced an adult fly. In the bottles where the males used were from normal stock, some of the eggs had produced larvae before they were counted and transferred

TABLE 2

Shewing the number of eggs laid and of flies hatched by fused females.

No. of culture	Parents ♀	Parents ♂	Eggs transferred	Larvae transferred	Adults produced
1	*fu*	*fu*	23	0	0
2	"	"	88	0	0
3	"	"	21	1	0
4	"	*N*	41	25	25
5	"	"	25	4	3
6	"	"	37	11	15
7	"	"	37	16	5
Total			272	57	48

to fresh food. The correspondence between the number of larvae produced previous to the transfer and of flies hatched, seemed to indicate that the eggs might have been injured by handling. To test this, fused females were mated with normal males and provided with food spread in a transparent layer upon glass slides so that the eggs when laid might be easily seen and counted without necessitating their removal. Every few days the eggs were counted and the slides with eggs untouched could be placed in new bottles with plenty of fresh food. The number of adults produced was very small (table 3) even with this careful treatment—in fact the percentage of adults hatched, compared with the number of eggs laid, is lower here (5 percent) than when the first method of treatment was employed (14 percent). Data from other sources show that the percentage of eggs which hatch in normal stock may vary from 20 to 90 percent of the number of eggs laid by any female.

It was formerly supposed that fused females were absolutely sterile. Besides proving this idea incorrect, an examination of table 2 revealed the fact that the three females which were mated with fused (*fu*) males gave no flies, while all four which were crossed with normal (*N*) males were slightly fertile. This is not correlated with the number of eggs laid, for one of the crosses of fused by fused yielded the largest number

TABLE 3

Showing the number of eggs laid and of flies hatched by fused females. Glass slide method.

No. of culture	Parents ♀	♂	No. of eggs laid	No. of flies hatched
B	*fu*	6 *N*	56	1
D	"	"	7	0
E	"	"	35	0
G	"	4 "	23	0
H	"	6 "	21	2
M	"	3 "	12	2
Q	"	"	38+	3
R	"	"	39	5
Total			231	13

(88 eggs) observed from any pair in the group. The significance of the kind of male used was then investigated by making a more extended series of crosses. That it is of importance, is shown by the fact that the combination of fused with fused never produced any offspring although 49 such females were tested by being mated singly with two or more fused males, while, on the other hand, out of 62 bottles of fused females by wild (*N*) males, only 13 (or about 21 percent) were totally unproductive.

As table 4 shows, many of the 49 fertile females produced but one adult while others gave as high as 30 and 36 flies; but in the sum total of 560 offspring not one male was found.

That bar-eyed males were as effective as the normal when used as mates for fused, was proved by crossing them with twelve fused females and obtaining 263 flies. Two of the fused females, or 16 percent, were sterile. Again, all of the F_1 were females (table 5). Combined with the data listed in tables 2, 3 and 4, this gives 884 females and not a single male as the total number of offspring from 89 fused females, 76 percent of which (68 individuals) were fertile to at least a slight degree, provided they were mated with males from strains other than their own. As fused is recessive, the F_1 females were normal or bar.

The presence of a dominant factor in the hereditary complex of fused individuals does not alter the sterility of the females. Twenty-seven red-bar-eyed fused females, mated with red or eosin bar males gave no offspring although all carried the sex-linked dominant bar.

TABLE 4
Fused ♀ by wild ♂.

No. of culture	*N* ♀♀	*fu* ♂♂	No. of culture	*N* ♀♀	*fu* ♂♂
101	15		132	0	
102	32		133	8	
103	35		134	10	
104	30		135	1	
105	7		136	10	
106	29		137	25	
107	24		138	0	
108	2		139	10	
109	20		140	0	
110	8		141	15	
111	1		142	1	
112	2		143	3	
113	20		144	10	
114	11		145	3	
115	14		146	1	
116	5		147	5	
117	3		148	1	
118	2		149	15	
119	16		150	3	
120	1		151	36	
121	7		152	24	
122	1		153	16	
123	4		154	0	
124	1		155	21	
125	0		156	10	
126	0		157	4	
127	0		158	28	
128	0		160	0	
129	0		161	4	
130	0		183	0	
131	6		159	0	
Total			62	560	

b. *Search for a factor for sterility*

Although in these preliminary tests, designed to ascertain the degree of infertility of the fused stock, the results of using normal and bar males show that fused females are not to be classified as totally sterile, it is still evident that their performance is far below normal. Throughout the course of this investigation, it was constantly borne in mind that the disability here encountered might be due to the activity of a particular factor for sterility. If factors, distinct from those which

TABLE 5
Fused ♀ by bar ♂.

No. of culture	Bar ♀♀	Fused ♂♂	No. of culture	Bar ♀♀	Fused ♂♂
171	58		177	56	
172	20		178	25	
173	21		179	1	
174	10		180	2	
175	5		181	0	
176	65		182	0	
Total				263	

cause the mutations, control the productivity of the individual, we must suppose that the two kinds are closely associated in the germ cell if we wish to account for the constancy with which sterility accompanies the specific character. In other words, in order to cause such close linkage, the sterility factors must be situated in the same chromosomes as the mutant factors, probably not far removed from them. According to the theory of crossing over, it should be possible to separate the two kinds of factors if such exist, and obtain sterile races which do not show the mutation and *vice versa*. This theory is based upon the idea of the linear arrangement of factors in the chromosome threads and postulates that during some stage in the cell history, previous to maturation, when the maternal and paternal members of each pair of chromosomes twist about each other, they may permanently fuse at one or more points and when untwisting may break apart in such a manner that homologous sections of the two chromatin threads may be interchanged. If the point of fusion and breakage should occur in the interval between the loci of the factors under consideration, one of those factors would become incorporated in the opposite chromosome and the linkage between these factors would be broken. Thereafter, each one could affect the gamete to which it was distributed, free from the influence of the other.

In the absence of any definite knowledge as to the dominance or recessiveness of the sterility factor (the existence of such an entity being assumed) it becomes necessary to consider both possibilities. On the supposition that it is recessive, the fused female, with which we have been dealing, must have been homozygous for sterility, otherwise it would not have exhibited the character. A crossover which occurred in such an individual would be unavailing since, both chromosomes hav-

ing the sterility factor, this would simply be a trading of identical genes. It is in the normal female, heterozygous for fused (and for the sterility factor) that favorable conditions for effective crossing over exist. If the crossover did occur once, however, the fused female which received one chromosome free from the sterility gene, should be fertile,—at least to some extent, according to the degree of recessiveness, assignable to the sterility factor. In this case the attainment of an individual homozygous for the "not-sterile" factor would be unnecessary, for the female heterozygous for "not-sterile" should be able to found a fertile fused strain. However, the fact that the $\frac{N}{f_u}$ female does not seem to be quite as fertile as the pure normal individual, suggests that the influence of the fused gene or of the sterility factor accompanying it, is semi-dominant, at least in this particular chromosomal complex. If this be true, a fused female heterozygous for the sterility gene might be moderately productive. If the attainment of a fused female which would have a normal fertility depends upon its homozygosity in regard to the allelomorph of the sterility factor, an egg belonging to the crossover class must be fertilized by a sperm of similar chromosomal composition before the fertile fused race can be obtained. However, it is possible that if the sterility factor is dominant, or partly so, the crossover class may already exist and the "not-sterile" factor may be passing, undetected, through the fused stock. In this case the homozygous condition might be readily obtainable.

It is of interest to note a peculiarity connected with the method of producing the homozygous crossover class when dealing with a factor like fused. Ordinarily, in such an attempt, the heterozygous female could be mated with the recessive male and their F_1 offspring, exhibiting the recessive character, could be inbred on the chance that the crossover gametes might unite in the F_2. But where fused is concerned, outcrossing is always necessary. Fused by fused produces nothing at all. Fused females by foreign males give only females—and these are not fused. Inbreeding with the pure stock is impossible. Both kinds of individuals, both fused males and females must always be derived from the heterozygous female. In the latter type, however, the condition demanded for crossing over is always present.

Upon the conclusion of the experiments summarized in table 4, it was noted that certain of the pairs had produced quite a few individuals. As these pairs were regarded as the most likely progenitors of a fertile line,

should one be forthcoming, some of the heterozygous F_1 females from cultures 101, 103, 104, and 158 were mated with fused males and from the F_2 resulting, 63 pairs of fused brothers and sisters were made up. Here, just as in the preliminary experiment, the combination of fused with fused resulted in total sterility; showing that not one of the females had obtained by a previous crossover, either one "dose" of a dominant factor for not-sterile or two "doses" of a recessive factor for not-sterile, which would permit them to be fertile when tested by fused males. Including data given in the succeeding pages of this section, a total of 412 fused females was tested for fertility. Of these 170 were crossed with fused and the rest, 242, with wild or bar males. The highest number of offspring produced by any one individual was 86 which is far below the expectation from a fertile fly. On the assumption that the sterility factor is one unit from fused, one out of each one hundred eggs produced by a heterozygous female should belong to the crossover class of fused-fertile. If sterility is recessive, any fly formed from the crossover type of egg would indicate the fact by being fertile. If sterility is partially dominant, the homozygous recessive must be extracted before a completely fertile fused race is obtained. Fertilization of the crossover type of egg by any Y sperm gives a fused-fertile male and since there is no crossing over in this sex, the two genes remain associated during their residence in it. The union of an X sperm from this fused male with an egg of like constitution should accomplish the formation of the fertile fused female. The chances of such a meeting seem rather remote even among 412 trials, but it must be noted that should the crossover occur, the new combination of genes would remain united with as great tenacity as they formerly remained apart and, on the assumption that sterility is semi-dominant, might have travelled together for some time undetected in the stock.

c. *Production of but one sex by fused females*

One of the most striking points brought out by the work with fused, namely, that the females gave offspring belonging to but one sex, remained to be investigated. The suggestion that there might be some peculiarity inherent in the fused female which prevented her from producing males, made it pertinent to test the point. A solution of the problem was found by using non-disjunction.

Since the discovery of the occurrence of non-disjunction in Drosophila, by BRIDGES (1916), it has been known that females which possess an

extra sex chromosome, i.e., that have the unusual constitution XXY, can produce males of an exceptional kind which are formed by the union of a Y-bearing egg from the mother and an X-bearing sperm from the paternal parent, just the reverse of the ordinary process. If a fused XXY female were crossed with a normal male, we should expect the F_1 to give not only females but also the exceptional males unless the nature of the fused female prevented the formation of more than one sex. Accordingly a stock which carried the extra chromosome was so combined with the fused race that their F_2 would yield fused females, one-half of which would be expected to have three sex chromosomes, i.e., be XXY females.

One hundred and fifty-five of such individuals with eosin eyes were mated singly with red bar-eyed males. In the results from these tests the sterility was greater than in the crosses with the wild fly, as only 78 gave offspring. The expectation was that one-half or 39 of these should carry a Y chromosome and each of the 39 could throw the exceptional males. Five of these produced one to four exceptional males (table 6). These males had red and bar eyes and normal wings like the father, since their only X chromosome was obtained from the paternal parent which was red, bar and normal. This proves that it is possible for males to be produced from fused females. There were obtained also 744 bar-eyed females but no fused males, although the two classes are expected in equal numbers. Another exceptional class, that of the fused females, formed from an XX egg and a Y sperm, should also have appeared and in as large numbers as the bar-eyed males, but it was not found.

So far no fused female had ever given any offspring when crossed with males of her own kind, but in order to discover whether these XXY females might not behave differently and throw the exceptional classes, 81 fused females, half of which were expected to carry the extra Y, were mated with bar fused males (red-, white-, or eosin-eyed). No flies whatever were produced. Copulation was observed to occur in some cases and that it may be partially effective is demonstrated by the following observations.

In making counts of the eggs it was noticed that on the second day after having been deposited some of them have a small black spot at the anterior end, indicating that the chitinous larval mouth parts are formed. Removal of the chorion reveals the fact that segmentation of the body has taken place and cuticular hooks have been formed. Pressure upon the cover glass over the object may rupture the body wall and a

TABLE 6

Fused ♀♀, half of which should be XXY, by bar ♂♂.

No. of culture	Bar ♀♀	Bar ♂♂	No. of culture	Bar ♀♀	Bar ♂♂	No. of culture	Bar ♀♀	Bar ♂♂	No. of culture	Bar ♀♀	Bar ♂♂
B 1	57		L 6	6		S 34			S 73		
B 2	10		L 7			S 35	4		S 74	1	
B 3			L 8	8		S 36			S 75	1	
B 4	82	4	L 9	11		S 37			S 76	2	
B 5	6		L 10	11		S 38			S 77	1	
B 6	3		L 11			S 39	7	1	S 78	1	
B 7			S 1			S 40			S 79	7	
B 8			S 2	11		S 41			S 80	4	
B 9	24		S 3	19		S 42	6		S 81		
F 1			S 4			S 43	14		S 85		
F 2	2		S 5			S 44	4		S 86		
F 3			S 6	5		S 45			S 87	4	
F 4			S 7	4		S 46	1		S 88	3	
F 5			S 8			S 47	2		S 89		
K 1	5		S 9	1		S 48	2		C 1		
K 2	10		S 10	14		S 49	4		C 2		
K 3			S 11	9		S 50	5		C 3	2	
K 4			S 12	7		S 51			C 4	7	
K 6			S 13	4		S 52	2		C 5		
K 7	24		S 14	17		S 53	2		C 6	1	
K 8	1		S 15	36		S 54			C 7	3	
K 9	17		S 16	1		S 55	1		C 8		
J 1			S 17			S 56	1		C 9	21	
J 2			S 18			S 57	4		K 10		
J 3			S 19	3		S 58	2		K 11		
J 4	1		S 20	2		S 59	4		K 12	22	
J 5			S 21			S 60			K 13	5	
J 6			S 22	1		S 61			K 14		
J 7			S 23	19	1	S 62	3		K 15		
J 8			S 24	4		S 63			K 16		
J 9			S 25			S 64	1		K 17	36	
J 10	14		S 26	7		S 65			K 18		
J 11			S 27	32	2	S 66	4		K 19		
J 12			S 28	1		S 67			B 10		
J 13			S 29			S 68			B 11	25	
L 2			S 30	1		S 69			B 12		
L 3			S 31		1	S 70	12		B 13		
L 4	8		S 32	1		S 71	3		B 14		
L 5			S 33			S 72	1		B 15		
Total									155	744	9

tube, identified as the alimentary canal, may be squeezed out. After the second day the eggs begin to darken and show signs of disintegration.

In only two cases out of hundreds observed, have larvae hatched from the eggs and never have they been seen to pupate. The lethal influence, therefore, of the pair of fused genes may not have its full effect until the egg stages, or even the larval period, is reached.

d. *Discussion of peculiarities shown by fused*

In interpreting the foregoing results certain striking facts brought out by the experiment must be kept clearly in mind:

1. In spite of more than two hundred attempts, no cross of fused by fused has ever been successful although fused males are ordinarily fertile with females of other races and fused females may in some cases lay a good many eggs and may even produce adults when mated with males from other strains.

2. The sygotic combination of fused with fused is not fatal, as is shown by the fact that females heterozygous for fused, mated with fused males, will produce approximately as many fused males and females as they will yield normal males and females. Only a negligible difference between the two types is to be observed.

3. In the crosses of fused females with males of different kinds, only females (plus a few exceptional males) were produced, although as many as 1628 females have been obtained.

4. That the lack of males is not due to any inability of the fused females to form that particular sex, was demonstrated by using XXY females and producing, through non-disjunction, males of the exceptional class, having the characteristics of the paternal instead of the maternal parent.

An examination of the various types of crosses in which fused has been concerned, reveals the additional fact that success, or at least partial success, ensues only in those cases in which a normal allelomorph of fused is involved at some point in the scheme though not necessarily present in either of the gametes at the time when they unite to form the zygote. We are, therefore, inevitably led to the conclusion that the deleterious influence of the fused gene is of such a nature that it must—and can to some extent—be counteracted by that of its normal allelomorph in the other X chromosome, in order to insure the production of adults. Furthermore, we see that the normal X chromosome may exert its opposing influence at two points: (1) it may be effective as a member of the parental complex, i.e., in the oögonial cell before maturation, as in the instance of the heterozygous fused female where it effects the

formation of a large number (almost the normal number) of eggs, and these are capable of being fertilized by sperm even though the latter may carry the harmful fused gene; (2) when present in a gamete from a male, the normal X may have the ability to "redeem" an egg produced by a homozygous fused female and to enable it to develop normally.

One other consideration is necessary to complete an explanation for all the phenomena cited in the preceding paragraphs. This relates to the nature of the Y chromosome. The experiments indicate that it contains nothing which can counterbalance the injurious influence of the fused factor at either of the above-mentioned points. Not only does it lack this counterbalancing power itself, it cannot gain such power from association with a normal X. These considerations furnish an explanation of the facts found in a detailed analysis of the crosses made. Reference to figure 1 may make the subject clearer by giving a visual image of the types of chromosomal combinations obtained.

FORMULA 1.—*A normal female heterozygous for fused by a fused male.* All four of the expected classes, normal and fused, males and females, appear. The normal allelomorph of fused,—or of a factor for sterility lying near fused,—is carried in the normal X of the heterozygous female and is sufficient to cause the production of a large, though not quite the normal, number of eggs. It restores the eggs carrying the fused gene so that the two kinds are produced in approximately equal numbers and both are viable in combination with either the Y sperm or the sperm carrying the factor for fused in the X chromosome.

FORMULA 2.—*A fused female by a fused male.* No offspring have ever been given by this combination, which seems to be dependent on the fact that neither the eggs nor the sperm contain a normal allelomorph of fused in their chromosomal constitution. Sperm from a fused male are viable,—as witness the preceding cross; eggs from a fused female may be fertile, — note the succeeding cross; the combination of two fused gametes can also occur; the only difference to be observed between this case and the first is the absence of the normal allelomorph of fused in the maternal complex and to this circumstance must be imputed the failure to obtain any offspring.

FORMULA 3.—*A fused female by a normal male.* A single class of individuals appears,—the normal females. As we have seen, the egg production of the fused female is below normal but does not cease entirely. In type 2, the X sperm carrying fused proved unable to form a viable zygote in conjunction with an egg which had not been under

the influence of a normal X. That the X sperm from a normal or bar male possesses this ability, is demonstrated by the occasional appearance of normal-winged females in the F_1 of this cross. The non-appearance of males must be attributed to the inability of the Y sperm to serve a like function.

FORMULA 4—*A fused female (XXY) by a bar-eyed or wild-type male.* Normal-winged females and males are given by this cross. Since maturation in this type of female differs from that of the normal, in several features, we may take up the analysis in more detail. Four kinds of eggs are expected to be formed: One with a single X chromosome which carries fused; one with two X chromosomes, each carrying fused; one possessing a fused X and a Y; one with a Y. The two kinds of sperm are the same as in the preceding cross,—one with a not-fused X, the other carrying a Y. The relationships here are similar to those in the case just discussed except for the addition of the Y in the maternal complex. As in the preceding case, only those individuals appear which are the result of a fertilization by an X sperm. This includes two types of females (XX and XXY) and the exceptional male (YX). No tests were made to distinguish whether the females actually were of different constitutions. Females containing XXX have never been found in any cross and are not expected here. The exceptional males, of which a small number were obtained, are formed by a union of an egg containing a Y with a sperm having a not-fused X. The greatest number of individuals given by any one female was 86 (table 6), which is slightly more than obtained from type 3 (tables 2, 3, 4, and 5), but by no means approaches the number produced by a female containing a normal X. This indicates that the Y chromosome cannot function like the normal X in the maternal complex in counteracting the effect of fused. It is evident that it possesses nothing which can overcome this harmful activity in the prematuration stages. The number of exceptional males expected is 4 percent of the total. Using the record of the most productive female for our computation we find that when 82 represents the number of F_1 females, the expectation for the exceptional males is 3.57. Actually 4 males appeared,—a very close approximation.

Fertilization by the Y sperm did not prove successful in a single case. The YY combination is not expected since it is supposed not to be viable, but that the X egg from a fused female is not fertilized by the Y, is explained by our assumption that the Y sperm does not con-

tain any property that can restore fused eggs nor can it acquire power so to do by association during spermatogenesis with a normal X.

FORMULA 5.—*A fused female (XXY) by a fused male.* No offspring whatever are produced. Eggs from such females and sperm from this type of male have proven viable in the preceding experiments. The particular gametic combinations expected are not impossible of realization under the proper conditions, yet no F_1 individuals are obtained. The explanation lies in the fact that the influence of the fused gene is not combated by the presence of its normal allelomorph either during oögenesis in the female or after the process of fertilization by the sperm.

RUDIMENTARY

a. The theories of prematuration and repugnance

The case of rudimentary wings, another sex-linked gene, located at 55.1 in the first chromosome, presents a less extreme example of the same sort of phenomenon as fused. The sterility of the females has been reported already by MORGAN (1912) and the theory of "prematuration" and "repugnance" suggested in connection with it. The first results indicated that the two cases possessed many similarities. MORGAN found that rudimentary flies when mated with rudimentary, were sterile; that rudimentary males were fertile with long-winged females; and that rudimentary females when fertilized by normal males gave a few offspring of both sexes. The only difference which destroys the parallel between the two cases, is in regard to the last point, for the F_1 of the fused female comprises only females while that of the rudimentary female represents males and females. It is true that most of the progeny were females, but a few males were found, in the ratio of about 1 : 300. A quotation will give MORGAN's conception of the element of prematuration.

"In the *heterozygous* female the egg has developed up to the time of the extrusion of the polar bodies under the influence of *M* (i.e., all the normal factors are present, at least in simplex) . . . Not until the time of polar-body formation is the factor *M* lost from half of the eggs, i.e., from those eggs that may produce rudimentary offspring. Hence the relatively large number of eggs that may be fertilized by the rudimentary-winged male. On the other hand in the *rudimentary* female the egg develops without the presence of the factor *M*. If the absence of this factor, in the prematuration development, makes the egg less fertilizable by any sperm, the difference in the behavior of the two kinds of females in question can be accounted for."

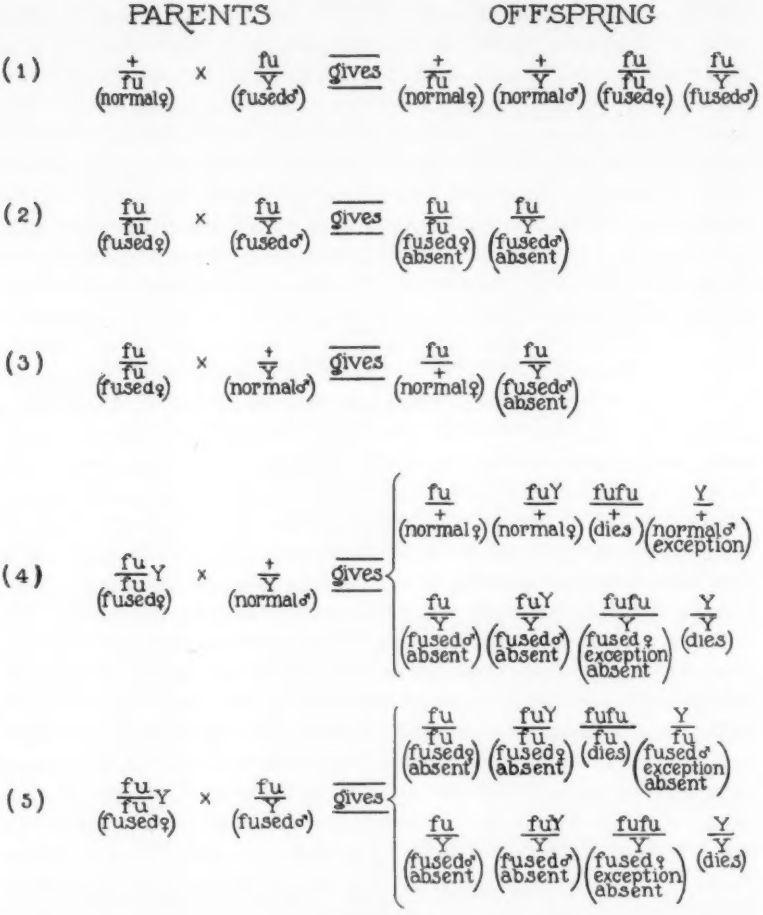

FIGURE 1

FIGURE 1.—Formulae of crosses testing fused flies. Each symbol represents a separate sex chromosome. Fused X = fu; not-fused X = +.

By the theory of "repugnance," MORGAN endeavored to explain the fact that in crosses between a female, heterozygous for rudimentary, and a normal male, the rudimentary class fell below expectation. He suggested that there was a repugnance between the rudimentary-forming gametes, that is, between the gametes which lack *M*. (In

referring to the original paper, it must be kept in mind that the terminology of the presence and absence theory was used and where the statement is made that "sperm lacking the character *M*, fertilizes with difficulty eggs lacking that same character," the Y sperm is considered to be "without" the above-mentioned *M* in the same way that the rudimentary-bearing egg is "without" it.) Statistics which prompted this explanation were given for a number of cases. In the first, there were 2061 miniature males and 479 rudimentary miniature males, a ratio of about 4.3 : 1 where a 1 : 1 ratio is expected. In the second, there were 342 miniature males to 98 rudimentary miniature, a ratio of 3.5 : 1. Several others gave ratios of 2 : 1 and 3 : 1.

MORGAN calls attention to the fact that his results represent an "improvement in the viability" of the rudimentary stock since its discovery. At first it had yielded 115 rudimentary males to 4773 (calculated) normal males, when equality was expected. Additional data published several years later (MORGAN and TICE 1914) showed that the disparity between the two classes of flies was due to unfavorable culture conditions rather than to a principle of repugnance. When overcrowding in the culture bottles was avoided, little repugnance was shown between any gametes forming the rudimentary classes either male or female. My observations on five matings of heterozygous females by rudimentary males, in which comparatively small numbers were involved, agreed with those of MORGAN and TICE. The total for five bottles gave 459 normal to 406 rudimentary males and 425 normal to 345 rudimentary females where equality is expected (table 7).

In the case of fused also, the principle of "repugnance" may be said to be inapplicable as is shown by the results given in table 1 from a similar cross where equality of the four classes is expected.

TABLE 7

Females heterozygous for rudimentary, by rudimentary males.

No. of culture	N♀♀	*r*♀♀	N♂♂	*r*♂♂	Total
900	124	80	130	136	470
901	102	90	108	88	388
902	96	95	119	91	401
903	69	40	56	45	210
904	34	40	46	46	166
Total	425	345	459	406	1635

In a later paper published by MORGAN (1915) the data for certain successful matings between rudimentary males and rudimentary females seemed to cast doubt upon the hypothesis of prematuration. The same type of cross in the fused stock, i.e., fused females by fused males, has never been attended with success except so far as to produce one or two larvae. That rudimentary by rudimentary may occasionally give offspring might be regarded as merely indicating that the injurious influence of the rudimentary gene is not so far-reaching as that of the gene for fused, without contradicting the general principle that particular genes may affect to a greater or lesser degree, the formation of the egg in the stages prior to the maturation divisions.

The principle of "restoration" outlined in the case of fused, is amply illustrated in the following experiment. The addition of a Y chromosome to the ordinary complex of the rudimentary female has an effect upon the formation of future classes similar to that obtained in the case of the non-disjunctional fused female, as the following data show. Sixty-five XXY rudimentary females (each X having a rudimentary gene) were mated separately to bar males (table 8). Fifteen bottles were sterile. The remaining fifty bottles gave 647 bar females, 2 rudimentary females, 41 bar males, and 52 rudimentary males. The four expected classes are represented by the four types obtained. An analysis of the cross may make this clearer. As explained in the case of the similar experiment with fused the XXY rudimentary female parent possesses three sex chromosomes, so that synapsis may occur in two ways (figure 2). There may be an XX synapsis and the Y may either pass out into the polar body or remain in the egg, thus forming eggs containing one X, or an X and a Y. In the second kind of synapsis the X is paired with the Y and the other X may pass out of, or stay in, the egg, forming gametes of the constitutions XX or simply Y as well as the XY and X classes. From analogy with other data, we assume that the XY eggs should comprise 46 percent of the total, the X eggs 46 percent, and the XX plus the Y 8 percent. All of these eggs should normally be capable of fertilization by either the X- or the Y-bearing sperm with two exceptions: the Y eggs fertilized by a Y sperm and the XX eggs by the X sperm, do not produce viable zygotes. Successful fertilizations by the Y sperm produce the recessive rudimentary classes.

In analyzing this cross, we find a second indication that the influence towards sterility of the rudimentary gene is not as great as that of fused, both because rudimentary males are obtained and because 2 rudimentary

TABLE 8

Red rudimentary XXY females by bar males.

No. of culture	Rud.	Bar ♀♀	Bar ♂♂	Rud. ♂♂	No. of culture	Rud. ♀♀	Bar ♀♀	Bar ♂♂	Rud. ♂♂
575					610		3		
576		50			611		7		
577		53	2	2	612				
578		8			613		11	1	
579		4		1	614		7		
580					615		12		1
581					616		26	2	3
582		13	1		617		3		
583					618		11		
584		16		2	619		1		
585					620		18	6	
586					621		1		
587					622		4		
588		35		3	623		5		1
589		26	3	6	624		18		1
590					625		17	1	4
591		2	1		626		4		
592					627		7		
593					628		35	2	1
594					629		6	3	1
595		13		1	630		6		
596					631		6	1	
597		9		1	632		43	9	14
598					633		6	2	1
601		1			634		9		
602		1			635		43		2
603		3		1	636		27	1	1
604					637		25		2
605		1			638	2	12	2	
606			1		639		1		
607		10			640		1		
608		3	2		641		16	1	1
609		8		2					
Total					65	2	647	41	52

exceptional females appear. The two corresponding classes have never as yet been obtained from any fused female. Here, the number of each is, however, below expectation. The rudimentary males should equal the bar females instead of being 52 to 647. This comparison, therefore, may be taken as a measure of the "restoring" power of the normal allelomorph of rudimentary. The X- and XY eggs which are produced by the rudimentary parent, all carry rudimentary and are of the same sort, no matter whether they are destined to be fertilized by an X- or a Y-bearing sperm.

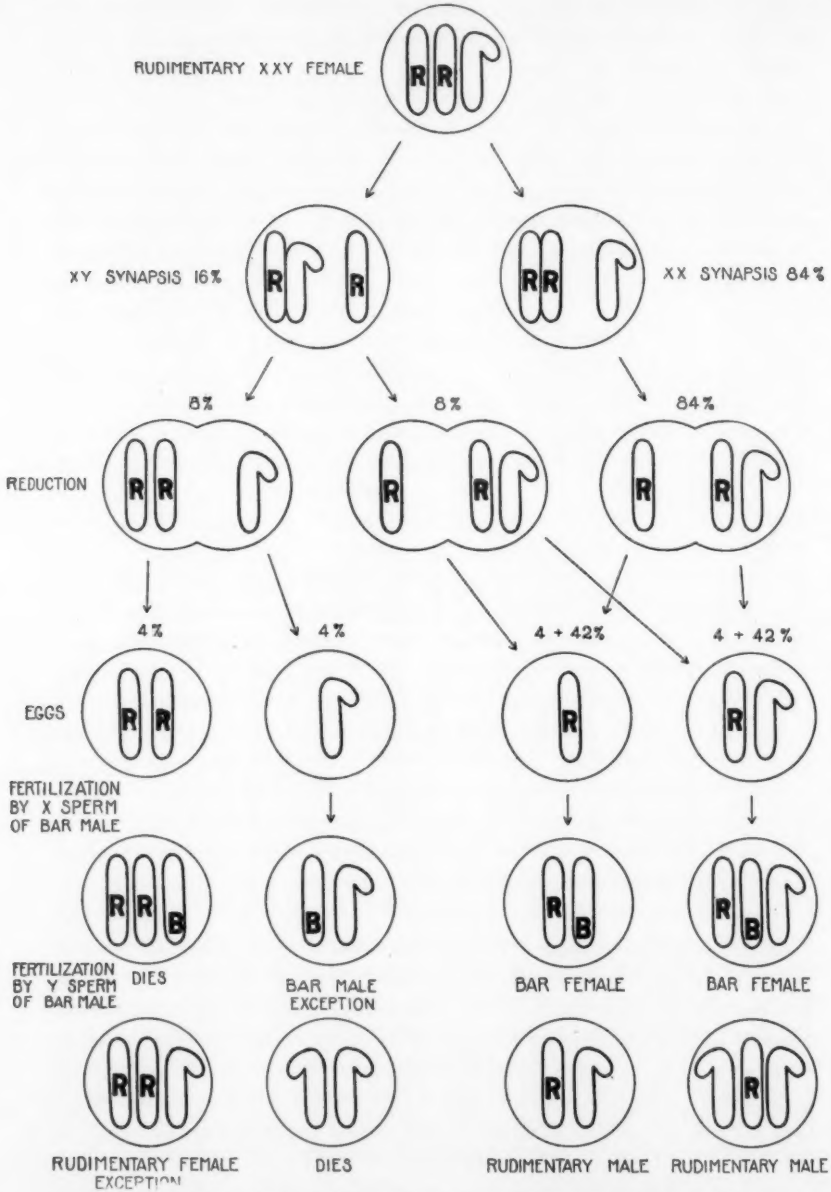

FIGURE 2.—Diagram showing the chromosomal constitution of an XXY rudimentary female, the two types of synapsis which occur in such an individual, reduction, the four possible kinds of eggs and the zygotes which would result from the fertilization of these eggs by sperm from a bar male. The X chromosome is represented as a straight rod and the Y as J-shaped. R = rudimentary, B = bar.

The zygotes formed from the two types of fertilization differ greatly in viability. The male zygotes are markedly fewer in number than the female. The Y chromosome which is brought in by the male-producing sperm, contains nothing, *ex hypothesi,* which can alter the viability of the egg. It does not change the percentage of sterility. The number of rudimentary males resulting from the XY and XYY zygotes is one-half the number which represents the degree of viability of the rudimentary egg when unaided by any influence from the sperm. We must suppose that a larger number of females than males is produced because the X-bearing sperm, which form the females, contain the normal allelomorph of rudimentary and have the ability in some degree to counteract the prematuration effect of the rudimentary gene upon the egg and to restore the normal process of development. The number of bar females produced compared with the number of rudimentary males, i.e., 647:52, is a measure of the "restoring" power of the normal allelomorph carried by the X sperm and operating after fertilization.

The two exceptional classes are the bar males and the rudimentary females which should be equal to each other and together should comprise 8 percent of the total progeny. The eggs which form these two classes are the result of an XY synapsis which is followed by the inclusion of the second X in the same cell with the first X, thus giving two types of eggs, —one with two sex chromosomes, XX, and one with but one sex chromosome, the Y. The first type of egg fertilized by a Y sperm, makes a rudimentary female; the second type fertilized by an X sperm, makes a bar male. This type of synapsis occurs in 16 percent of the total but as one-half of the possible zygotes derived from it are not viable, the individuals of either exceptional class are 4 percent of the total number of fertilizations by either an X sperm or a Y sperm. For example, the bar males compared to the bar females should be as 4 percent is to 92 percent, and the rudimentary females to rudimentary males should also be as 4 to 92. The total output of eggs is far below normal, probably due, as has been previously suggested, to the adverse influence upon development, of the rudimentary gene. There is no reason to suppose that the ratio of the various classes would be changed in any way from that expected in any cross involving non-disjunction. A comparison of the number of bar males to the bar females obtained, is perfectly legitimate in that the principles of both prematuration and restoration are at work in the type of union which results in the formation of both classes. A computation based on such a comparison gives 28 as the number of

bar males expected. Actually there are 41. The fact that the percentage of non-disjunction is known to be variable may account for this disparity.

In the type of reproduction which gives the rudimentary males and females, only one principle is in action—that of prematuration. As the sperm concerned in these fertilizations carries a Y as its only sex chromosome and does not possess any element to combat the injury of the prematuration influence, the principle of "restoration" is absent. Therefore, fewer rudimentary females are expected than bar males, although under normal circumstances the classes should be equal. As previously stated, the rudimentary females should be to the rudimentary males as 41 is to 92. The numbers actually obtained (2 to 52) are in quite close agreement with expectation.

b. *Search for a factor for sterility*

In continuation of the search, begun in the case of fused, for a gene governing fertility and distinct from that of the mutation involved, it was deemed advisable to test some of the individuals of the previous experiment to see whether a fertile race of rudimentary flies could be obtained. The rudimentary females from the above cross died before they were tested in regard to fertility. The other females were long-winged and had to be mated with rudimentary males in order to produce rudimentary offspring which in turn could be tested for fertility. This was done and 100 of the rudimentary females thus obtained were mated in mass cultures with their rudimentary brothers and 75 were crossed with bar males from stock (table 9). If, by means of a crossover in the heterozygous female the rudimentary gene had become separated from a sterility gene, some of these females tested might reflect this event by producing a large number of offspring. However, none of them gave as many individuals as the grandparents, one of which had yielded as many as 66 flies (table 8).

c. *Additional mutations to rudimentary*

Rudimentary has appeared twice in other stocks kept in the laboratory. One of these mutations to rudimentary, found by Mr. D. E. LANCEFIELD (1918), was tested by crossing five rudimentary females with bar males. No offspring whatever resulted, indicating that this second mutation to rudimentary was also accompanied with sterility. Whether a previous mutation to sterility had occurred at a point adjacent to the rudimentary locus, and was made apparent only by the modifying action of the rudimentary gene is a question not settled by the evidence.

TABLE 9

Rudimentary ♀♀ by rudimentary or bar ♂♂.

No. of culture	Parents ♀♀	♂♂	F_1 ♀♀	F_1 ♂♂	Total
702	11	× 6 rud.	1	2	3
703	6	3 "	3	1	4
704	10	5 "			
705	4	12 "	3	10	13
706	3	4 "			
708	11	6 " +1B'	10	8	18
709	4	2 "	3	8	11
710	3	3 "			
711	9	7 "	18	±5	±23
713	10	10 "	6	7	13
719	12	7 "	2	5	7
714	10	10 "	6	5	11
720	7	7 "	2		2
715	33	13 B'	20	3	23
716	18	7 "	28	7	35
717	22	33 "	13	8	21
718	2	2 "			
Total	175		115	69	184

Dr. A. H. STURTEVANT found rudimentary a third time; in this instance, in a strain of black purple curved flies. A cross between this newest rudimentary and a normal female heterozygous for the original rudimentary gene gave normal and also rudimentary males and females. Had the new mutation been dependent upon a gene different from the first, their F_1 should give only normal offspring, as each parent would carry in its chromosomal constitution the normal allelomorph for the opposite factor. Since the recessive class of rudimentary females appeared in the F_1 we must conclude that each parent contributed the same gene and that the third mutation of rudimentary was therefore identical with the first.

The STURTEVANT stock was then tested for the possible occurrence of a fertile individual. Of 72 females, crossed with bar males, none yielded more than 57 offspring and 45 (about 62 percent) did not reproduce at all (table 10). The sterility here seems to be more pronounced than in the first rudimentary stock but this is perhaps to be referred to temperature conditions rather than any real difference in the nature of the gene. This strain was kept up by mating some of the heterozygous females with rudimentary males and the tests were continued upon their offspring. Twenty-seven of the rudimentary daughters were mated with one or

TABLE 10

Rudimentary ♀♀ by bar ♂♂ (STURTEVANT stock).

No. of culture	Bar ♀♀	Rud. ♂♂	Total	No. of culture	Bar ♀♀	Rud. ♂♂	Total
1001				1037			
1002				1038			
1003				1039		1	1
1004				1040			
1005				1041			
1006	1		1	1042	11	2	13
1007				1043	2		2
1008				1053	5		5
1009	1		1	1054	+		+
1010				2002			
1011				2001	+		+
1012	1		1	2003			
1013	5		5	2004			
1014	2		2	2005	1		1
1015				2006	3		3
1016				2007			
1017				2008	1		1
1018				2009			
1019				2010	1		1
1020	1		1	2011			
1021	2		2	2012			
1022				2013			
1023				2014	2		2
1024				2015			
1025				2016			
1026	1		1	2017			
1027				2018			
1028				2019	1		1
1029				2022			
1030				2023	2		2
1031				2024			
1032				2025	2		2
1033				2026			
1034		2	2	2028	+		+
1035	2		2	3221	31	26	57
1036				3225	+		+

more rudimentary brothers (table 11) and 14 of these bottles gave offspring. Nine rudimentary females, out-crossed with bar males, all reproduced, but none of either of these groups gave more than a dozen flies (culture No. 4095 to 4103, inclusive). In addition 94 rudimentary females were crossed with bar males (Nos. 4020 to 4105 and 4152 to 4160). An exact record of their performance was not kept but a large number of offspring was not given by any one of them. Among the 202 females of the STURTEVANT strain, tested for sterility, a completely fertile individual was not found.

TABLE II

Rudimentary ♀♀ by rudimentary ♂♂ (STURTEVANT *stock*).

No. of culture	♂ and ♀ offspring	No. of culture	♂ and ♀ offspring	No. of culture	♂ and ♀ offspring
3251	2	3240	3	3248	1
3252	1	3243	2	3249	1
3236	2	3245	2+	3250	4
3237	2	3246	3	3262	1
3239	3	3247	8		

Thirteen other cultures gave no offspring.

MORULA

"Morula" eye is dependent upon a gene located at 106.3 in the second chromosome. It is characterized by great irregularity in size and protuberance of the ommatidia. In addition, the reduction of the bristles on the thorax is of such regular occurrence that their condition may be taken as diagnostic of morula when the eye disturbances are scarcely detectable.

The females lay only a few eggs. Five, which were observed for ten days, gave respectively 0, 0, 4, 9, and 4 eggs, none of which hatched. The males are probably perfectly fertile as no difficulty is experienced in keeping up stock by means of crossing them with the heterozygous female.

As the female shows a very high degree of sterility, it is evident that the few eggs which are laid are seldom capable of normal development. Three hundred morula females were mated with morula males in small mass cultures. No offspring were obtained. In order to discover whether males, other than her own kind, were more effective as mates, which had been observed to be the case with fused, 107 bottles were made up, each containing one female and 1 to 3 red bar or eosin crimson males. With sterile stocks difficulty is often experienced with the growth of mold upon the banana used as food, which may prevent the development of flies that might come through if it were not for this adverse condition. In this experiment the expedient was tried of inoculating the 107 bottles with the eggs of yellow flies so that the larvae of the more viable stock might churn up the food and by their activity destroy the mold. The adults of this stock could easily be distinguished from any gray morula flies which might hatch at the same time. Even with this precaution, the percentage of fertility was not materially increased

as only one of the 107 females gave offspring. She produced but two individuals, both normal-eyed females. Crossing these heterozygous females with morula males gave normal and morula males and females. Some of the males had yellow bodies, showing that the original morula grandparent had been fertilized by one of the yellow flies with which the bottle had been inoculated instead of by a red bar or eosin crimson male. Probably, no particular significance attaches to this fact. Eighty-eight of the F_2 morula females were mated with morula brothers, either yellow or gray-bodied, but none of them reproduced.

These figures indicate the very high rate of sterility among morula females as only one individual in the 500 tested gave offspring. The same considerations in regard to the possibility of sterility being dependent upon a separate gene, apply here as in the case of fused or rudimentary. Each one of these females was derived from a heterozygous parent which fulfilled the conditions necessary for crossing over. Had a chromosome containing morula, but free from the factor for sterility, been made up during this process, the occurrence would have been detected in the individual formed from it, provided sterility is recessive. Even if it is semi-dominant, either by itself or as a modifier of morula, we might hope that the homozygous recessive, i.e., for fertility, might have been formed during so many tests. That no morula female evinced normal fertility must be taken to indicate that sterility is dependent upon a gene lying exceedingly close to morula or that it is one of the manifold effects of morula itself.

REDUCED BRISTLE

Among the mutant stocks which proved sterile was one named "reduced bristle" because of the fact that the bristles on the thorax are reduced either in size or number. Stock is kept up by mating the heterozygous female with reduced-bristle males as the reduced-bristle females showed a high degree of unproductivity.

Observations on the egg-laying capacity were made in but two cases. The first female laid no eggs at all during a period of 9 days and the second laid 77 in 11 days. None of these hatched.

Of 70 reduced-bristle females tested for fertility with Australian (wild type), bar, California (wild-type) or eosin crimson males, only three gave offspring, producing 1, 37 and 16 flies, respectively. The difficulty of obtaining males which was evident in the fused and rudimentary stocks was conspicuously absent here as No. 53 gave almost half again as many males as females, i.e., 23 to 14, and No. 54, 7 males to 9 females.

This fact is in no way a contradiction of our theory of "prematuration and restoration," but is rather a confirmation of it and is explicable on the ground that here we are not dealing with a sex-linked factor.

The homozygous reduced-bristle females, as we have seen, lay very few eggs. We assume this is owing to the fact that the harmful influence of the pair of reduced-bristle genes (or of the sterility genes lying adjacent to them) is unchecked by any normal allelomorph in the prematuration stages of oögenesis. Some of these eggs, however, may be fertilized and brought to complete development by the redeeming influence of the gamete from the male. Since reduced bristle is not sex-linked but lies in the second chromosome its normal allelomorph is contained in duplex in all males used in the experiment. Therefore, all sperm, whether X- or Y-bearing, also carry an autosome which possesses an allelomorph to reduced bristle (or sterility) and have the power to counteract, in some measure, the injurious reactions started in the egg by reduced bristle, and produce viable zygotes. Since both male- and female-forming sperm have this capacity, both sexes are represented in the F_1. As reduced bristle is recessive, the F_1 flies appear normal.

The three productive lines were continued by out-crossing some of the bar-eyed daughters heterozygous for reduced bristle, to reduced-bristle males from stock and the reduced-bristle F_2 females obtained in this way were tested to see whether they were fertile. Among the F_2, of line 53, 16 females were mated in small mass cultures with males of their own kind but produced no flies. Twelve females from line 54 and 25 from line 52 gave similar results, showing that in a total of 125 females, not one possessed the reduced-bristle factor free from a factor for sterility, although three of them were not totally sterile.

DIBRO

The name "dibro" is an abbreviation of the three principal characteristics: dichaete, beaded and rough, exhibited by one of the strains which proved sterile. Besides having reduced bristles, beaded wings, and irregular eye facets, the abdomen is noticeably shorter and smaller in circumference than in the normal fly. The stock died out before the gene was located in any chromosome. BRIDGES, who found this mutation, reports the appearance of only one male, which was sterile, and in my cultures the four males which appeared were so weak that they lived only a short time.

The ovaries of the dibro female are small and the eggs remain im-

mature. Observation of twelve females, mated with bar or dibro males, for periods of from 9 to 16 days showed that no eggs had been laid.

Three females mated with bar males produced no offspring during the five or six days which they lived. Five more, mated with bar males, also showed sterility. The mutation appeared in eosin-eyed cultures and stock is maintained by making a large number of pair matings from the bottle which threw dibro. The appearance of dibro from any one pair shows that each one of the parents must have carried the gene in question and indicates the proper line from which to continue the stock.

DWARF

Aside from the fact that they are often lighter in color than the normal stock, dwarf flies show few differences from the wild type except that implied by their name. Frequently they are smaller than the wild fly, being approximately one-half the normal size but the range of variability is very great and some individuals may overlap the normal. The eggs also are smaller than those of the wild fly. The long axis is considerably shorter giving the egg a chubby appearance. Not all the females lay eggs. Of the eight females mated with either bar, dwarf, or wild males, and placed under observation for various periods of time, three produced no eggs, the other five gave 143, 50, 143, and 108, respectively (table 12). In the batch of 143 eggs, 54 of them dried up and therefore must not be included in the fertility percentage. From the total of 291 eggs, all from crosses in which bar or normal males had been used, only seven flies hatched. They were either bar or normal females. It is to be noted that no males appeared, but this fact is probably not to be regarded as significant in view of the small numbers involved.

TABLE 12

Showing number of eggs laid by dwarf females and of flies hatched therefrom.

No. of culture	Parents ♀	Parents ♂	No. of days observed	Eggs laid	Flies produced
1	d_w	B'	6	0	0
2	"	d_w	12	0	0
3	"	N	12	89+54	4
4	"	B'	14	50	1
5	"	"	9	43	0
6	"	"	14	1	0
7	"	"	14	108	2
8	"	"	11	0	0
Total				345	7

In a previous experiment, in which no counts of the eggs were made, the fertility of 31 adults was tested and found to be zero. Two of the heterozygous females obtained from the group of 108 eggs in the egg-count experiment were mated to dwarf males and gave 160 normal flies to 21 dwarf females and 25 dwarf males. Twenty maroon dwarf females from this cross and 4 from another F_2 group, were placed with bar or dwarf males, but did not yield a single individual. To sum up, 3 out of 63 females proved slightly fertile.

CLEFT

Cleft (denoting a peculiarity in venation) is a sex-linked recessive (locus 65). Only males of this mutant type have appeared. Since they are sterile, it has not been possible as yet to obtain any cleft females. Stock is kept up by mating the daughters of any female which has thrown cleft.

Examination shows that the testis is usually misshapen, often with the parts more or less fused, but containing live sperm. Copulation has not been seen to take place. Seventy-four males were put in separate bottles to which were added females from California (wild type), Australia (wild-type), bar or eosin crimson strains and, in two cases, normal females heterozygous for morula. These bottles had previously been inseminated with larvae from yellow stock in order to keep the food in good condition. Four of them gave a few offspring but until tested it was not certain whether their paternal parent had been a cleft male or a yellow male that had chanced to hatch early. When the female offspring mated, the kind of males they produced would indicate their ancestry, for both cleft and yellow are sex-linked and would therefore appear in the F_1. The results of the test of the daughters gave yellow males in every case, but no cleft, proving the paternal parent to have been yellow.

In regard to the possibility of separating an (assumed) sterility factor from that of cleft it is to be noted that the separation could not take place in the male, since crossing over does not occur in the male of Drosophila. In the heterozygous female from which cleft males were derived, however, fertile sons might be produced. In the seventy-four tests made such an individual was not discovered.

GENERAL DISCUSSION

The words fertility and sterility are blanket terms, covering a wide variety of conditions and descriptive of the degree of activity of a physiological function. The terms do not stand for an allelomorphic

pair of genes. We may suppose that every species has achieved, during the course of evolution, a characteristic mechanism for propagating its own kind that has sufficed to effect its survival. This process of normal reproduction entails numerous complexities, the omission or dislocation of any one of which might bring about sterility. In many cases the sterility might be accidental and not transmissible from parent to offspring. On the other hand, it is evident that a large number of either physiological or morphological differences affecting the formation or growth of the germ cells, or the mechanism connected with their liberation or fertilization, might upset the normal function of reproduction and be dependent upon some chemico-physical basis in the germinal constitution which would be passed on from one generation to the next as a true hereditary factor. Any departure from the normal may alter the balance of the reaction either towards an improvement over the condition ordinarily maintained or towards a less favorable one. If "fertility" expresses the normal condition, definitions may readily be found for such terms as "high fertility," "partial sterility," etc., the normal always being retained as the standard of comparison. In a case like fused, the two conditions found in the female of complete sterility with its own males and partial fertility with males from other strains are probably both the manifestations of a single determining cause in the germ cell. Here, the number of individuals which reproduce and also the number of offspring from each individual, is affected.

At present, it is not possible to state definitely whether the determining causes for the cases reported in this paper, consist of separate genes which have sterility as their principal somatic expression or whether they are an integral part of the genes responsible for the associated character, but the latter seems probable. It is evident that we are dealing with the activity of some factor and not concerned with inbreeding, with heterozygosity or the proportion of dominants present, all of which conceptions have been proposed as explanatory of various instances of sterility or fertility.

The sterility of three of the mutants reported here, rudimentary, fused, and reduced bristle, is evidently of the same type and may be elucidated by reference to the same theory. Morula, dwarf, cleft and dibro present no contradictory features. The fact that cleft is sterile in the male sex is readily harmonized with our theory on the assumption that the injurious influence of the cleft gene in the heterozygous female is so severe that it extends to the males produced by her, thus making them incapable of producing offspring.

The most clear-cut case is that of "fused" and a detailed inquiry re-

veals something of the mode of operation of the sterility connected with it. We have seen that the influence that causes the sterility is progressive, not acting with finality upon all of the gametes at any one point, but making itself felt throughout development. At two points in the process it is capable of being counteracted by its normal allelomorph. The harmful reactions (or inhibition of proper activities) set up by the gene, operate during oögenesis, in the stages previous to maturation and result in the production of a very small number of eggs unless their effect is checked by the presence of the normal allelomorph in the maternal chromosomal complex. In case the normal allelomorph is absent during prematuration, the few eggs laid perish unless the sperm which fertilize them bring in the normal allelomorph and restore to a certain percentage of them the usual course of development. The result will be that some of the females will produce a small number of offspring. When a sex-linked factor, such as fused, is concerned, the allelomorph is contained only in the X chromosome, i.e., the female-forming type of sperm, and therefore the F_1 from a fused female results in females only. In the case of a non-sex-linked factor, like reduced bristles, either sperm may carry the normal allelomorph in the autosome so that both sexes are comprised in the filial generation. On the same principle, morula and dwarf would be expected to yield some F_1 males if larger numbers were involved.

Rudimentary does not afford such a clear-cut case as fused but analysis of the data shows that the same principles are at work as in fused although the harmfulness of the latter gene is greater than that of rudimentary. A few rudimentary males may be formed when rudimentary females are fertilized by normal males and the cross of rudimentary by rudimentary is sometimes partially successful. But that the difference between rudimentary and fused is one of degree rather than of kind justifies us in including them in the same general category.

An interesting comparison, though not an exact parallel, in regard to the possibility of a prematuration influence, is afforded by the case of self-sterility in Nicotiana, reported by East and Park (1917). The non-occurrence of self-fertilization is explained by reference to the fact that male and female gametes have developed in the same individual and therefore under the influence of identical factors. Incompatible crosses are due to "the likeness of the parents in the effective hereditary factors postulated." The male gametes themselves may be of different kinds yet none can fertilize eggs from the same—or a similar—source as themselves. The prematuration influence in these plants appears to

be dependent upon the presence in the parental complex of a factor for self-sterility together with an unknown number of additional genes instead of being narrowed down as in the case of fused to the influence of one particular factor. The analogy of the cases does not extend to the conception that the identity of parental constitutions, regardless of the gametic type, is responsible for the phenomena observed but merely that the sterility is determined by activities in the diploid cell prior to maturation.

The experiments with fused have demonstrated that the Y chromosome is beyond the influence of the factors in the X chromosome. Recent considerations on the structure and formation of the Y chromosome, published by MULLER (1918), indicate that it is an accumulation of recessives, the product of degenerative changes in the factors. On this basis, it would not be expected to contain a gene in the locus corresponding to that of fused in the X chromosome that would be even remotely related to it. The behavior of the Y chromosome here, showing that it cannot be influenced by fused nor counteract the influence of fused upon other parts of the cell, is in accord with MULLER'S work.

While an exhaustive search for sterility factors is still to be completed, certain facts concerning the nature of the element at work have been pointed out, whether these peculiarities are to be regarded as dependent upon the presence of a distinct entity, the sterility factor—or factors—or whether they are but additional manifestations of the mutant genes themselves. All of the cases investigated appear to belong to the same type, the most clearly defined instance being that of fused. The corroborative evidence furnished by the latter suffices to rehabilitate the discarded theory of prematuration and although the principle of repugnance has not been substantiated an additional one has been suggested, namely, that of restoration.

SUMMARY

1. Males of the following races are fertile: fused, rudimentary, morula, reduced bristle, and dwarf. Cleft males are sterile.

2. Of the few individuals of dibro which were tested, both males and females were sterile.

3. When mated with males of their *own* race, fused and morula females are sterile, rudimentary females are partially so.

4. When mated with males of *other* races, a certain percentage of morula, dwarf, reduced bristle, rudimentary or fused females may give a few offspring; in a few cases morula and dwarf produced a very small number of individuals, all females; occasionally reduced bristle may

reproduce, giving a small number of each sex; rudimentary may yield a larger number of individuals, with females predominating; from 413 fused females, 1628 females and no males (except a few produced through non-disjunction) have been obtained.

5. In no case has it been possible to isolate a factor for sterility independent of the mutant factor itself. In each case the sterility shown is, therefore, probably one of the manifold effects of the gene responsible for the mutation.

6. The sterility involved decreases not only the number of fertile individuals in each race but also the number of offspring produced by each fertile female. However, the harmful effect of the mutant gene upon the egg may be counteracted at two points in the history of the gamete: (1) in the prematuration stages of oögenesis, that is, if the female is heterozygous for the mutant gene, a larger number of individuals will be produced than if she is homozygous; (2) if, at the time of fertilization, the sperm brings in the normal allelomorph, even though the female is homozygous and the number of eggs consequently reduced, a larger number of offspring will result than when the sperm carries the mutant gene. The Y chromosome has no corrective influence.

7. No "repugnance" has been observed between the gametes forming the recessive mutant classes.

I wish to acknowledge my indebtedness to Professor T. H. MORGAN for his helpful criticisms during the course of these investigations. I wish also to express my appreciation of the valuable suggestions of Dr. C. B. BRIDGES and Dr. A. H. STURTEVANT.

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ON VARIATION IN TARTARY BUCKWHEAT, *FAGOPYRUM TATARICUM* (L.) GAERTN.[1]

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[Received June 21, 1919]

TABLE OF CONTENTS

PAGE

INTRODUCTION 534
Materials and methods 535
Description of the normal and abnormal flowers 538
Analysis of data 542
First generation 542
Second generation 547
Third generation 548
Fourth generation 550
Fifth generation 557
Periodicity in the manifestation of the characters of the ever-sporting variety 558
Frequency distribution of different types of flowers with regard to position on the plant 560
Frequency of occurrence of different types of flowers in relation to the different periods of the flowering season 565
Fasciation in *Fagopyrum tataricum* 568
Observations on the influence of the environment upon teratological development in *Fagopyrum tataricum* 574
SUMMARY 583
LITERATURE CITED 585

INTRODUCTION

From the morphogenetic point of view the manifestation of dimorphism in certain races of plants,—the so-called ever-sporting varieties,—presents a very interesting problem. The remarkable feature of these races is the constancy with which the two diverging forms of the same organ are transmitted in ever-sporting fashion; no breeding method has, as yet, been conceived by which, for instance, certain variegated types of plants or certain strains of Matthiola, could be induced to breed true. These races appear as compound forms ever transmitting the potentialities of the two component types.

[1] Papers from the Biological Laboratory of the MAINE AGRICULTURAL EXPERIMENT STATON No. 131.

Dimorphism manifests itself in two externally different forms. The different, "mutually exclusive" characteristics may appear simultaneously distributed in the organs of the same individual as in *Trifolium pratense quinquefolium, Veronica agrestis*; in another group of plants each individual of the race may display only one of the dimorphic characters as in the case of certain strains of Matthiola, Antirrhinum, *Dipsacus sylvestris torsus*, etc.

In interpreting these phenomena, DE VRIES, whose investigations involved a great abundance of material, assumes the peculiar behavior of these races to be due to the interaction of two "antagonistic, mutually exclusive, characters." The operation of these two contending characters within the individual leads to the formation of two distinct groups of plants, the half-races and the middle races or ever-sporting varieties. Opposed to this interpretation is the view held by certain writers who consider the ever-sporting nature of many of these races as mere somatic variations and relegate them into the group of non-heritable modifications.

More recently, however, some of the ever-sporting types in plants as well as in animals have been subjected to a genetic analysis and their peculiar mode of inheritance has been explained in terms of Mendelian factors.

The purpose of the present publication is to record the results of a study on a highly variable, ever-sporting race which the writer has discovered in *Fagopyrum tataricum* Gaertn. (*Polygonum tataricum* Linn.). This race was isolated in 1916 and five generations have been growr since. In the course of his observations on this race the writer's attention was chiefly devoted to the study of variation and transmission of the external characters in an endeavor to establish first by direct experiment the hereditary behavior of this race under different conditions before attempting an analysis of the underlying genetic causes. The study of the phenotypic expression of the characters of this new race has furnished enough interesting data and observations to warrant their publication.

MATERIAL AND METHODS

The race with which this paper is concerned originated from commercial fruits of *Fagapyrum tataricum* Gaertn., Tartary buckwheat, also known as India wheat, which had grown in Maine. While examining these fruits preparatory to planting in the spring of 1915, the writer's

attention was attracted by a rather high number of fruits whose structure differed from the normal triangular type in that they possessed a quadrangular and, some of them, a quinquangular form. In the spring of 1915 these abnormal fruits were planted along with several hundreds of normal fruits in rows in the cereal-breeding garden of this STATION at Aroostook Farm. The rows were one foot and a half apart and the individual plants stood 3 inches apart within the rows. To guard against any possible interference on the part of insects the plants were covered with cheese-cloth screens.

Frequent examination of the flowers borne by each of the plants originated from the abnormal fruits in the summer of 1915, revealed a high degree of variability in the number of carpels. Deviation from the normal number of perigone members was also noticed. Each of these plants was harvested separately and the fruits examined. The plants showed a varying degree of variability in the number of abnormal fruits. The precise ratio between the number of normal and abnormal fruits could not be established, as some of the fruits had been lost before the plants were examined. However, in all cases the number of abnormal fruits did not equal that of the normal ones. One plant was found to be distinguished by a particularly high degree of variability in the shape of its fruits. This plant was selected as a starting point of a strict pedigree culture in 1916. The strain descended from this original plant will be referred to here as line 5.

For the purpose of comparative study, an apparently normal strain of Tartary buckwheat designated in our record books as line 22 was selected in the same year and grown ever since along with the highly variable line 5 under the same environmental conditions, as a control line.

In order to test these strains in as many generations as possible in the course of a few years the development of these races was continued over the winter in the greenhouse. This afforded the further advantage of permitting the study of the race under different conditions of environment. As will be seen later certain environmental conditions have a very marked influence upon the range of variation of the characters of this race. Indeed, the regularity and uniformity of response of the cultures to certain conditions of environment seem to throw some light upon the releasing agents that are involved in the manifestation of the variation and in the control of its scope in this race. A description of the different conditions of environment will be given later in connection with the analysis of the data on each generation.

The methods used in the examination of the material and in recording the data may here be briefly outlined. The variability of the race in question affects the number of carpels and perigone leaves. In regard to recording the number of carpels two methods have been used. The first one, the simpler of the two, consisted in the examination of all fruits of each plant and in their distribution in groups according to the number of angles of the fruits. As the angles of the buckwheat fruit correspond to the midribs of as many carpels, the number of angles of a fruit is equivalent to the number of carpels of the flower from which the fruit had originated. After sorting the different fruits into groups the individuals of each group were counted and the ratio of the different groups established. Over 44600 fruits were recorded by this method.

This method, while relatively simple and convenient, does not reproduce an absolutely exhaustive and truthful picture of the entire range of variation. For, as will be seen later, the more extreme variants of this race, the flowers with higher numbers of supernumerary carpels, are sterile. Consequently the statistical examination of the ripe fruits does not reveal the entire range of variation which by neglecting the extreme variants, i.e., the sterile flowers with a high number of supernumerary carpels, is manifestly narrowed down to forms more closely approaching the normal type. However, the extreme variants are rather rare and their exclusion from consideration affects the ratio between the total numbers of normal and abnormal flowers to only a slight degree. A complete picture of the range of variation embracing the full amplitude of the aberrant forms is obtained by the laborious method of picking and examining the flowers successively as they appear on the plant. The difficulty of this method is at once obvious if the smallness and structure of the flowers of *Fagopyrum tataricum* are recalled. In order to determine the number of carpels, each flower was examined with the aid of a hand lens and the number of stigmas counted. In connection with the study of the distribution of abnormal flowers upon the plant as well as for the purpose of determining the complete range of variation of this race, over 12000 flowers were examined by this method. In all, upward of 57000 flowers and fruits were examined in the study of this race.

Before considering the data it seems advisable to give a description of the morphology of the normal and abnormal flowers of this species.

DESCRIPTION OF THE NORMAL AND ABNORMAL FLOWER

The flowers of *Fagopyrum tataricum* are normally borne on axillary simple racemes. The normal flower is typically trimerous except the perigone, which consists of a whorl of 5 similar green leaves with a yellowish tinge. The androecium is composed of two whorls of stamens. The outer whorl bears five leaves which according to EICHLER (1876-1878) developed from an originally trimerous whorl by reduplication of two of its members. The inner whorl consists of three stamens. In contrast to the dimorphic heterostyly of the common buckwheat, *Fagopyrum esculentum,* the flowers of Tartary buckwheat are homostyled, the relation between the height of the stamens and pistils being the same in all individuals of the species. The stamens of the outer whorl are usually incomplete with anthers scarcely developed. They seem to play no part in the pollination process. This is entirely left to the three stamens of the inner whorl. In examining such large numbers of flowers the writer invariably found the pistil to be very closely surrounded by the inner stamens; their anthers adhere to the stigmas of the carpels and upon bursting cover them with pollen, thus insuring self-fertilization of the flower. This self-fertilizing mechanism of the flower of *Fagopyrum tataricum* makes this species far better adapted to the study of inheritance of its characters than the heterostylous *Fagopyrum esculentum,* since it offers no difficulty in raising pure-line cultures.

The gynoecium is normally composed of three carpels which unite to form a triangular ovary. Each carpel is only slightly prolonged into a very short style terminating with a stigma. The normal fruit is a triangular achene or nutlet (figure 1, first fruit in upper row).

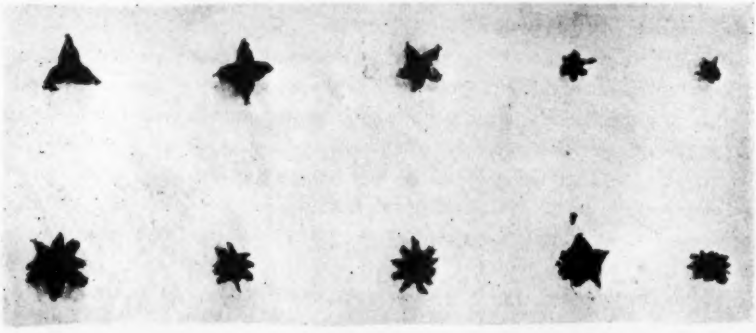

FIGURE 1.—Fruits of an ever-sporting strain of *Fagopyrum tataricum* with supernumerary carpels varying in number from 3 to 12. × 1.8.

The abnormal flowers occurring in this race show a great diversity of forms. The abnormal condition of the flowers affects chiefly two floral organs, the gynoecium and the perigone. It also affects the number of flowers per individual pedicel as in the case of the so-called synanthous flowers. The characteristic feature of all abnormalities occurring in this race is that they represent deviations from the normal extending only in the plus direction.

Before describing the main forms of the abnormal flowers we may note the scant references recorded in the teratological literature regarding variation in the flowers of *Fagopyrum tataricum.* It may be stated in advance that a careful survey of the literature revealed only a single reference regarding variation in the number of carpels of *Fagopyrum tataricum.* PULLMAN (1905, p. 11), in his account of observations on *Fagopyrum esculentum,* calls attention to the occurrence of flowers with more than three carpels giving rise to achenes with four, five and more angles. In this account he makes a brief statement that "many-angular fruits also occur in *Fagopyrum tataricum.*" No other record regarding abnormalities in the gynoecium of *Fagopyrum tataricum* has come to the writer's notice. Nor are references concerning the abnormalities in the gynoecium of *Fagopyrum esculentum* and in the Polygonaceae in general, to be found more frequently in the literature. While PULLMAN makes the first direct reference regarding supernumerary carpels in the gynoecium of Fagopyrum, the phenomenon was known, though not recognized as such, as far back as 1829 when LOISELEUR and DESLONGSCHAMPS (cf. PENZIG 1894, p. 265) found an unusually enlarged ovary of *Fagopyrum esculentum* which they erroneously described as a new species, *Polygonum pyramidatum.* This was undoubtedly a syncarpous gynoecium formed by supernumerary carpels. WEBER (1860, p. 365) mentions generally the occurrence of an increased number of carpels in Polygonum. BENTHAM (1865, p. 714) describes the flower of Polygonum as having 2 or 3 styles, the fruit being, accordingly, flattened biangular, or triangular. Further references regarding the abnormalities in the gynoecium of the different forms of Polygonum sp. are found in PENZIG'S "Pflanzen-Teratologie." Thus in *P. persicaria* the style is 2-3 cleft, the achene bi- or triangular. In *P. orientale* a gynoecium has been observed with two whorls of carpels. CLOS (cited by PENZIG 1894, p. 265) mentions a case of adesmy of the carpels in the same species. In the gynoecium of *P. tinctorum,* two instead of the normal number of carpels occur.

While it is of interest to note these instances of instability in the structure of the gynoecium in the different forms of Polygonum, it is equally obvious that these deviations from the normal type occur only very rarely and that their range of variability is very limited. Concerning the variation in the number of perigone leaves, the writer is not aware of any previously recorded observation in regard to *Fagopyrum tataricum* or *Fagopyrum esculentum,* though a few instances of such variations have been noted in other forms of the Polygonaceae (cf. WEBBER 1889).

The abnormal flower form most frequently encountered in our race possesses a gynoecium composed of 4 carpels giving rise to a quadrangular achene. Frequently associated with this quadri-carpellate gynoecium is a perigone consisting of six instead of five leaves. As will be noted later, over 25 percent of all examined four-carpellate flowers bore six-parted perigones. Less frequently occurring are the five-carpellate flowers of which about 24 percent were found to bear six-parted perigones. Flowers with 6-10 carpels occur fairly frequently in this race. Flowers with 11, 13, and 15 carpels are of rare occurrence. A few flowers were observed with as high a number of carpels as 19 and 20. One flower was noted with a gynoecium composed of 25 carpels and bearing a perigone of 18 leaves. This flower marked the most extreme variant observed in this race. The number of supernumerary members of the perigone varies up to 14 although a few flowers were found with 16 perigone leaves. Eighteen perigone members were the highest number observed. Figure 1 presents a series of abnormal fruits originated from flowers with 4-12 carpels taken from one plant. Figure 2, A, B, C, represent flowers with 6, 7, and 8 perigone leaves.

As the number of supernumerary carpels increases their frequency decreases. In a flower with 8 or more carpels the shape of the gynoecium appears modified. The gynoecium loses its angular structure, the numerous, crowded carpels make it appear larger and more globular presenting on cross-section a wavy circular line. Very often these floral monstrosities show at the apex an aperture of varying width (see figure 3, A). In some extreme cases the ovary is entirely open, forming at the top a more or less elliptical ridge which is lined up with the stigmas of the numerous carpels. As a rule the flowers with over 7 or 8 carpels are sterile, but very frequently the ovary of these flowers increases considerably as seen in figure 1, lower row, and assumes the appearance of a developed fruit, only to wither within a short time.

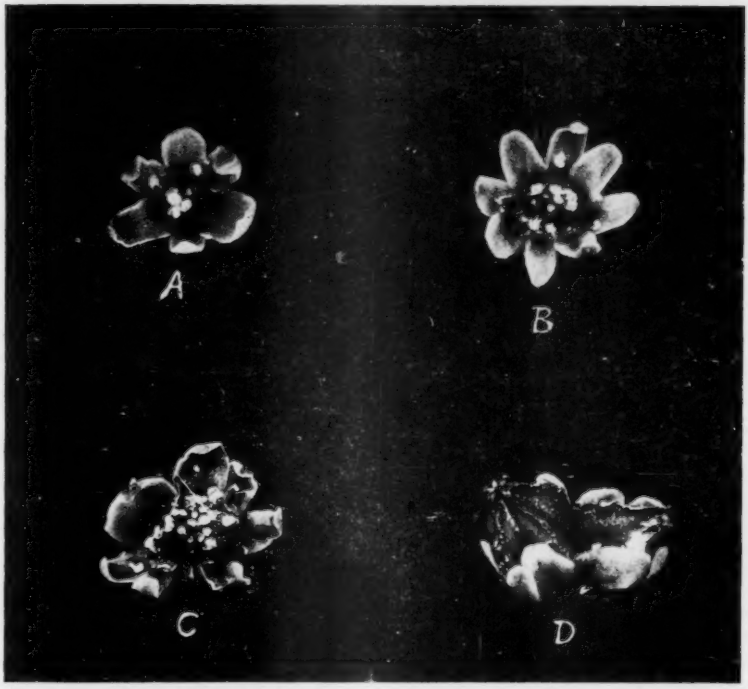

FIGURE 2.—Abnormal blossoms of *Fagopyrum tataricum*.—A. Flower with six-parted perigone. B. Flower with eight-parted perigone. C. Flower with seven-parted perigone. D. A case of syncarpy. The fruit to the right is normal, triangular, the one to the left is abnormal, five-angled. The stigmas of the carpels are still noticeable at the summit of the fruits. All × 5.

Before closing the description of the abnormal flowers attention may be called to another abnormality which hitherto has not been recorded for *Fagopyrum tataricum*. While in the abnormal flowers, considered above, the gynoecium bears the semblance of a single pistil, in the cases to be now considered, the flowers show two or three distinct pistils. Two forms of these abnormal flowers can be distinguished. The torus of the flower may appear unusually enlarged, and on its surface two or three distinct pistils may appear. All the pistils, however, are surrounded by a common perigone composed of numerous leaves. These flowers are naturally large and can be easily detected on the plant even in bud condition.

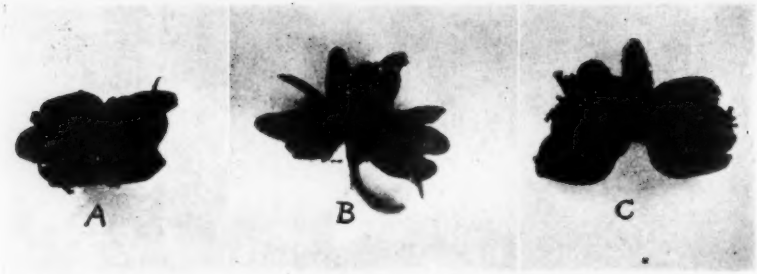

FIGURE 3.—Abnormal blossoms and fruits of *Fagopyrum tataricum*. A. A monstrous fruit with 12 carpels, viewed from above. The carpels did not fuse at the summit, leaving a distinct, elliptical aperture. This type of fruit is invariably sterile. B. An interesting illustration of synanthous development involving 3 flowers. C. A case of synanthy involving two highly abnormal flowers. Each flower appears surrounded by a separate perigone. All × 5.

The second form, more frequently met with, presents a structure known as "synanthy." Two or three complete flowers are borne on a single, broadened pedicel and are surrounded by separate perigones. Synanthous flowers with two pistils (figure 3, C) occur rather often in this race while synanthies involving three flowers as shown in figure 3, B, are of rare occurrence. Regarding the structure of the flowers forming the synanthies it is of interest to note that, as a rule, they are themselves abnormal in that their gynoecium is composed of more than three carpels. In a few rare cases where one member of the synanthy developed a normal triangular pistil the other member was invariably found to possess abnormal pistils composed of more than three carpels. In cases where the number of carpels in the gynoecium of the synanthous flowers was comparatively low the flowers often developed to maturity giving rise to syncarpous fruits (figure 2, D). A more detailed account of the different forms of synanthy occurring in this race will be given in another paper.

ANALYSIS OF DATA

First generation

The data to be considered here will be presented in chronologic sequence in connection with each of the five generations of this race.

The first generation of the original plant selected in 1915 was grown in the greenhouse of the UNIVERSITY OF MAINE in the winter of 1916. In order to determine the effect of nutrition upon the production of ab-

normal flowers, the fruits were subjected to different cultural treatment. A part of the fruits was planted in an 8-inch pot, No. 2, filled with normal garden soil which had been mixed with ordinary commercial fertilizer. In the second series the other portion of the fruits was planted in pot No. 2a containing soil that had been mixed with a considerable amount of sand.

Regarding the other conditions of environment, they were alike for the cultures in both pots. The temperature of the greenhouse was kept at 70-75 degrees Fahrenheit (21-23.8° C.).

The examination of the flowers as they appeared on the plants revealed a high degree of variability in the structure of the gynoecium and perigone. In table 1 are given the frequencies of the different flower forms found on the plants grown in fertilized soil, in pot No. 2.

TABLE 1

LINE No. 5.—*Frequency distribution of the number of flowers with respect to the number of carpels.*

	Number of carpels												
Plant No.	3	4	5	6	7	8	9	10	12	14	16	Synanthies	Total
1	33	119	15	4	1	3	1	1	1			2	180
2	39	147	31	13	2	8			2		1	3	246
3	58	222	51	17	1	4	4	5	3	1		6	372
4	35	117	22	3			1	2			1	1	181
5	40	126	28	10	2		1	2				3	213
Total	205	731	147	47	6	15	7	10	6	1	2	15	1192
Percentage	17.21	61.33	12.33	3.94	0.50	1.26	0.59	0.84	0.50	0.08	0.17	1.26	

From these figures it is evident that the number of abnormal flowers is far in excess of that of the normal ones, the percentage ratio being 17.21 : 82.79. The flowers with four carpels show the highest frequency, constituting 61.33 percent of all flowers and 74.06 percent of all abnormal flowers. The percentage frequencies for all five plants are graphically represented by the solid-line curve in figure 4. It is a bilateral curve whose apex is determined by the four-carpellate flowers. The short left flank of the curve is determined by the normal flowers while the abnormal variants form the extended right flank of the curve.

In examining the figures in table 1 and the corresponding curve in figure 4, it may be noted further that while the frequency distribution as a whole decreases with the increasing number of carpels per flower, the flowers with an even number of carpels occur more frequently than

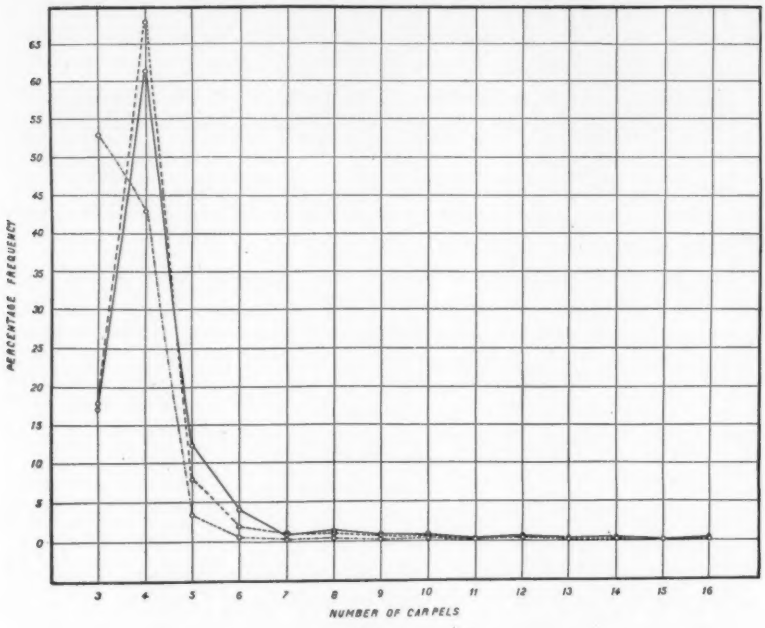

FIGURE 4.

those with an odd number of carpels from the six-carpellate flower on. Flowers with 11 and 13 carpels are of very rare occurrence while flowers with 15 and 17 carpels have not been observed either in this or in the following generations. To be sure, the number of flowers in the higher polycarpellate categories is small but it is of interest to note that this tendency of the anomalies to produce more pistils of an even number of carpels than those of an odd number has been maintained in all generations of this race in which the more extreme anomalies have been produced. This tendency, as will be clearly seen from figure 4, interferes with the regularity of the curve of variation.

Associated with the variation in the number of carpels in the flowers of this race is a comparatively moderate degree of variability in the number of the perigone leaves. At the time when the data on the first generation were collected the variations in the perigone were also noted, but the data do not represent the exact numerical relationship between the different categories of the perigone forms as they were not recorded

until sometime later when it was discovered that their occurrence was more than accidental. It is in connection with the study of the fourth generation of this race that an exact statistical examination of the variations in the perigone was made. The data as they were recorded for the first generation are given in table 2 in totals for all the five plants.

TABLE 2

Number of perigone leaves.....	5	6	7	8	9	10	16	Total
Number of flowers.....	1053	86	25	5	4	3	1	1177
Percentage	89.59	7.21	2.11	0.42	0.34	0.25	0.08	100

These figures clearly show that the frequency distribution of the flowers with the normal five-parted perigone prevails decidedly over those with abnormal perigones, the percentage ratio being 89.59: 10.41. Among abnormal perigones the six-parted perigone shows the highest frequency, 69.35 percent of all abnormalities. In accordance with numerous observations of DE VRIES (1910), HARRIS (1917), and other writers, the frequency distribution in this case decreases with the increasing degree of the deviation. This variation can be represented in the form of a skew or unilateral curve whose apex is formed by the normal five-parted perigone of the species.

The plants that grew in the unfertilized sandy soil were found to behave very much like the plants considered above. The statistical examination of these plants, 15 in all, with regard to the variation in the gynoecium, gave the results shown in table 3.

TABLE 3

Number of carpels	3	4	5	6	7	8	9	10	11	12	13	20	Total	Synanthies
Frequency ...	437	1436	300	63	8	18	9	10	3	6	1	2	2293	28
Percentage ..	18.83	62.62	13.08	2.75	0.35	0.79	0.39	0.44	0.13	0.26	0.04	0.08		1.22

A comparison of these percentage frequencies with those given in table 1 for the plants grown in fertilized soil shows that the behavior of the plants in both series in regard to the distributions of the corresponding categories of flowers is practically identical. The difference in the media in which the plants grew affected neither the numerical relationship between the different classes of variants nor the range of the variations.

Very similar conditions in both series of plants were found to prevail in the case of the variations in the number of perigone leaves. Table 4 gives the frequency distribution of the flowers with respect to the number of perigone leaves in the 15 plants grown in sandy soil in pot No. 2a.

TABLE 4

Number of perigone leaves	5	6	7	8	10	12	13	14	18	Total
Frequency	1994	217	43	17	5	4	1	1	1	2293
Percentage	87.13	9.35	2.28	0.73	0.22	0.17	0.04	0.04	0.04	100.00

It will now be of interest to turn our attention to the first generation of plants originated from fruits of the plant that appeared originally as a normal representative of the species as it had not produced any other than triangular fruits. The first generation raised from these fruits comprised 13 plants which grew alongside the first generation of the variable race considered above. The flowers of all the 13 plants were examined in the same manner as those of the variable race with the results given in table 5.

TABLE 5

LINE NO. 22.—*Frequency distribution of flowers with respect to the number of carpels.*

Plant No.	Number of carpels					Total
	2	3	4	5	6	
1		165	4			169
2	1	140	10		1	152
3	1	189	14	1		205
4		76	8			84
5		68	4			72
6	1	73	3			76
7		131	4			135
8	1	62	3			66
9		52	4			56
10		37				37
11		23	1			24
12		43				43
13		27				27
Total	4	1086	55	1	1	1147
Percentage	0.35	94.68	4.79	0.09	0.09	100

From table 5 it is evident that the 13 plants of line No. 22 exhibit an entirely different behavior from that of the variable line No. 5. The normal flowers of the species constitute in line No. 22 the bulk of the

flower output while the abnormal variants represent only 5.32 percent of all the flowers. With regard to the variations in the perigone leaves, 29 flowers out of a total of 1147 or 2.53 percent developed a six-parted perigone. While this strain may well represent the normal, slightly variable type of the species, its behavior under greenhouse conditions suggested a similarity with a number of strains which DE VRIES has named "half-races" in distinction from the ever-sporting varieties.

Second generation

In order to examine the behavior of the characters of these two lines, a limited number of flowers on the plants of the first generation were marked, to avoid repetition in counting, and permitted to mature. The matured fruits were harvested from each plant separately and planted outdoors in the spring of 1916. The fruits from plant 5, pot 2, of the ever-sporting line No. 5 and from plants No. 3 and 7 of pot 4, of line No. 22 were subjected to different cultural treatment. The fruits of each plant were divided into two parts; one portion was planted in pots (Nos. 15. 16 and 17) containing only gravel, while the other portion of the crop was planted in pots (Nos. 18, 19 and 20) filled with rich soil mixed with commercial fertilizer. A number of fruits from other plants of the first generation were planted in pots (Nos. 22, 23 and 24) filled with normal soil. All the pots were placed outdoors. The data on the variation of these plants were obtained by determining the number of angles of each fruit and then grouping the fruits into the different categories. In table 6 are given the data for the second generation of line No. 5.

A comparison of these figures with those on the first generation presented in table 1 shows a striking difference in the range of variation and in the numerical relationship between the different variants. The average percentage ratio between the normal and abnormal fruits in all the second-generation plants of this race is 62.85 :37.15 as against 17.21 :82.79 in the first-generation plants. No less affected is the range of variation which is narrowed down to six-angular fruits, i.e., six-carpelled flowers, as the most extreme variants. Thus our race under the conditions influencing the growth of the second generation not only failed to progress in the development of its character, but showed a very distinct reversion toward the normal type of the species.

The data on the second generation of the very slightly varying line No. 22 are given in table 7.

TABLE 6

LINE No. 5.—*Actual* (f) *and percentage frequencies of numbers of fruits with respect to their number of carpellary angles.*

Pot No.	Source of fruits	Medium	Number of fruit-angles								Syncarpies	
			3		4		5		6			
			f	percent	f	percent	f	percent	f	percent	f	percent
17	Plant 5, pot 2	Gravel	486	66.30	235	31.77	10	1.36	1	0.14	3	0.41
20	Plant 5, pot 2	Rich soil	864	66.72	295	30.50	34	2.62	1	0.08	1	0.08
22	Plant 4, pot 2	Normal soil	295	63.58	164	35.34	5	1.08				
23	Plant 3, pot 2	Normal soil	187	61.51	110	36.19	7	2.30				
24	Plant 10, pot 2	Normal soil	687	56.13	459	37.50	78	6.37				

TABLE 7

LINE No. 22.—*Actual* (f) *and percentage frequency of number of fruits with respect to their number of carpellary angles.*

Pot No.	Source of fruits	Medium	Number of fruit angles			
			3		4	
			f	percent	f	percent
15	Plant 3, pot 4	Gravel	222	99.10	2	0.90
19	Plant 3, pot 4	Rich soil	1839	99.73	5	0.27
16	Plant 7, pot 4	Gravel	175	100		
18	Plant 7, pot 4	Rich soil	1491	99.46	8	0.54
21	Plant 10, pot 4	Normal soil	470	100		

When compared with the data on the first generation given in table 5, these results show, as in the case of the ever-sporting line No. 5, that the conditions under which the second generation plants grew, narrowed the range of variation and favored the development of the normal type of flower or fruit. The average percentage ratio between the normal and abnormal fruits of the second generation plants is 99.66 : 0.34 as against 95.01 : 4.99 in the first generation.

Third generation

The third generation of the two strains was grown in the summer of 1917 under three different sets of environmental conditions. In the first series the fruits were planted in pots containing fertilized rich loam of Aroostook County, Maine, and were placed in the greenhouse at the AROOSTOOK FARM. The second series comprised plants originated from fruits that had been planted in pots filled with sand and gravel and placed outdoors. In the third series the fruits were sown in the open

TABLE 8

LINE No. 5.—*Actual* (f) *and percentage frequency of number of fruits with respect to number of carpellary angles.*

Pot or row No.	No. of plants	Source of fruits	Medium and location	Number of fruit angles																	
				3		4		5		6		7		8		9		10		Syncarpy	
				f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent
Pot 28	6	Plant 1, pot 20	Rich soil, greenhouse	1366	55.04	1000	40.29	112	4.51	4	0.16										
Pot 35	13	Plant 1, pot 20	Sand, outdoors	218	53.69	175	43.11	13	3.20												
Row 713	2	Plant 1, pot 20	Garden	833	61.84	485	35.78	28	2.17	1	0.07									2	0.14
Pot 30	4	Plant 1, pot 17	Sand, outdoors	256	42.67	205	40.17	47	7.83	2	0.33										
Row 715	2	Plant 1, pot 17	Garden	1098	51.07	949	44.14	83	3.36	7	0.33	4	0.19	2	0.09	1	0.05	2	0.09	4	0.19

TABLE 9

LINE No. 5.—*Actual* (f) *and percentage frequencies of number of flowers with regard to number of carpels.*

Plant No.		Number of carpels																													
		3		4		5		6		7		8		9		10		11		12		13		14		16		18		19		Synanthies		Total
		f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	
Pot 36	1	78	17.69	320	72.56	27	6.12	5	1.13	2	0.45	1	0.23	1	0.23	2	0.45	1	0.23					1	0.23							3	0.68	441
	2	49	14.41	249	73.24	17	5.00	10	2.94	1	0.29	3	0.82			1	0.29							1	0.29							9	2.65	340
	3	119	19.97	389	65.27	46	7.72	10	1.69	3	0.50	10	1.68	3	0.50	5	0.84			1	0.17											10	1.68	596
Pot 37	4	130	16.62	520	67.01	66	8.51	14	1.80	5	0.61	10	1.29	10	1.29	5	0.64			2	0.26					1	0.13					13	1.68	776
	5	136	20.80	430	65.60	51	7.80	8	1.22	6	0.92	7	1.07	1	0.15	3	0.46															12	1.83	654
	6	150	21.08	488	68.54	49	6.88	7	0.98	3	0.42	2	0.28	2	0.28	4	0.56															7	0.98	712
Pot 39	7	127	15.05	572	67.77	67	7.94	24	2.83	9	1.07	7	0.83	4	0.47	8	0.95			8	0.95	2	0.24							1	0.12	15	1.78	844
	8	190	17.48	719	66.51	101	9.34	15	1.39	6	0.56	7	0.65	6	0.56	13	1.20	3	0.28	5	0.46	1	0.09	1	0.09			1	0.09			13	1.20	1081
Total		979		3687		424		93		35		47		27		41		4		16		3		3		1		1		1		82		5444
Percent		17.98		67.73		7.79		1.71		0.64		0.68		0.49		0.75		0.07		0.29		0.06		0.06		0.02		0.02		0.02		1.50		

ground in the cereal garden. It should be noted that the fruits of each individual plant selected for the propagation of the race, were subjected to the three different cultural treatments.

In table 8 are given the summarized results obtained from the examination of the three series of plants of the third generation of the ever-sporting race.

From these figures it will be noted that the third generation of the ever-sporting variety also displayed a type and range of variation different from that of the first generation. The figures taken as a whole in conjunction with the data, not given in the above table, on a number of plants grown in the garden, indicate that the variation is unilateral, with the normal type of flowers prevalent over the abnormal flowers, though not so distinctly as in the second generation.

If we may assume the variation manifested by the plants grown in the garden to be typical of the third generation, the ratio between the normal flowers and the total of abnormal flowers was found to be 52.78: 47.22. The dash-and-dot curve in figure 4 illustrates the variation in the type of fruits of the third-generation plants grown in the garden.

The results obtained from the examination of the third generation of line No. 22 may be stated briefly. The series grown in pots filled with sand and gravel and kept outdoors comprised 23 plants which developed only triangular fruits, 381 in all. The data on the series grown from the same fruit fraternity in garden rows were based on the examination of 10 plants that yielded a total of 3191 fruits. Of these 99.47 percent were triangular, 0.44 percent four-angular, and 0.09 percent five-angular, fruits.

From a consideration of the three generations thus far analyzed it is evident that the variations shown by the second and third generation are significantly different from those of the first generation, notwithstanding the fact that in many points, notably the nutritional conditions prevailing in the second and third generation, the cultural treatment was very much like that in the first generation. This pointed strongly towards the existence of certain specific conditions prevailing in the greenhouse of the UNIVERSITY OF MAINE, where the first generation had grown, that might have operated in a manner favorable to the development of abnormal flowers in this race. With a view to testing the influence of these conditions the fourth generation of both races was grown again in the UNIVERSITY greenhouse, in the winter of 1917-'18, under conditions as nearly identical with those of the first generation as possible.

Fourth generation

The bulk of the fourth-generation plants originated from fruits borne by plants that had grown in the summer of 1917, in pot No. 26 in the greenhouse at the AROOSTOOK FARM, and which had yielded 2754 fruits, 48.17 percent of which were triangular, 46.07 percent four-angular, 5.73 percent five-angular, and 0.04 percent six-angular. The kind of fruits and nutritional stratum for the raising of the fourth generation were selected in a manner that promised to furnish some evidence relative to a few problems that have developed in the course of the study of line No. 5. For the continuation of this race from generation to generation four-angled fruits were chiefly used, but in some cases, where three-angled fruits were used, it was noted that their offspring did not differ markedly from that raised from four-angled fruits of the same plant. It was thought desirable to obtain some evidence on this question by the examination of the material furnished by the fourth generation. In connection with the study of the fourth generation an attempt was also made to determine the periodicity, if any, in the occurrence of abnormal flowers or fruits of this race at different flowering periods of the plant. This problem will be dealt with in a separate section of this paper. Finally, the inquiry into the effect of optimum and deficient nutrition upon the variation of the flowers was continued in the fourth generation.

With these problems in mind, three-, four- and five-angled fruits of the same fruit fraternity from pot No. 26, were planted separately in three pots, Nos. 36, 37, and 38, respectively. All the three pots had ordinary garden soil as a common growth medium. Another part of fruits of the same crop was planted in pot 39 filled with composted soil, while still another portion of the crop was planted in pots 42 and 48 filled with sand.

The fruits for the continuation of line No. 22 were taken from the third-generation plants that had grown in the summer of 1917 in plot 777, row 738, in the cereal garden, yielding 99.28 percent of three-angular, and 0.72 percent of four-angular, fruits. Some of the three-angular fruits of this plant were planted in pot 46 filled with composted soil. In connection with the determination of the effect of environment upon the variation in the flowers a number of other pot cultures were grown but they may be passed over here as they will be referred to when the question of the influence of environment will be discussed in another section of this account. All the pots were placed closely together on the south side of the UNIVERSITY greenhouse.

Three plants each from pot 36 and 37 and 2 plants from pot 39 were selected for the study of the periodicity in the frequency occurrence of the abnormalities. The flowers of these plants were examined and recorded daily, including Sundays, by the method previously pointed out. The flowers of 2 plants in pot 38 were also examined in the same way, but not recorded daily, as they were not included in the material for the study of the periodicity in the occurrence of the different forms of flowers. The flowers on the remaining plants in each of the pots mentioned above were left unmolested to maturity when their fruits were examined and their different forms recorded. Thus by examining the variability of two sets of plants grown in the same pot and raised from the fruits of the same plant, each by a different method, it could be determined to what extent the method of counting and examining the ripe fruits followed in the analysis of the second and third generation approached the exhaustive picture of variation obtained by the counting and examination of the flowers.

The data collected by examining all the flowers, 5444 in all, on some of the plants in pots 36, 37 and 39, are regarded here as representing the type and range of variation of the fourth generation of this race. The actual and percentage frequencies of the different flowers of the fourth generation plants are presented in table 9.

A comparison of these figures with the data on the first generation given in table 1 at once reveals a striking similarity of type and range of variability in the two generations, thus bearing out the assumption made above. The average percentage distributions of the flowers of the first- and fourth-generation plants, given in the lowest horizontal array in both tables, are practically identical, indeed, they are in more complete accord with each other than the corresponding distributions of flowers on plants grown in the same pot in each of the two generations. While there is a slight variation in the numerical relationship of the abnormal variants of both generations, the percentage ratio between the normal flowers and all abnormal flowers is practically the same, being 17.21 : 82.79 for the first generation and 17.98 : 82.02 for the fourth generation. The similarity of the variability in the first and fourth generations is graphically represented by the dashed and solid curves in figure 4.

It may be argued that these highly concordant results obtained for the first and fourth generations as well as the much higher degree of variability of these as compared with the second and third generation, may be due to the fact that in the examination of the first and fourth generation

the method of picking and examining the flowers was used while the results for the second and third generation were obtained by examining the ripe fruits. It is also conceivable that the traumatic stimulation caused by the daily removal of the flowers may have influenced the degree of development of the abnormalities. It will, therefore, be instructive to consider now the results obtained from the examination of these plants from pots Nos. 36, 37 and 39, whose intact flowers were permitted to develop into fruits which were examined at maturity in the same manner as in the case of the second and third generation. Table 10 gives the summarized results for 7 plants from each pot.

TABLE 10

LINE No. 5.—*Actual* (f) *and percentage frequency of number of fruits with respect to number of carpellary angles.*

Pot No.	No. of plants	Number of fruit-angles										
		3		4		5		6		8		
		f	percent	f	percent	f	percent	f	percent	f	percent	Total
36	7	32	23.02	84	60.43	19	13.67	4	2.88			139
37	7	25	17.60	95	12.68	18	12.68	2	1.41	2	1.41	142
39	7	31	15.66	157	79.29	9	4.55	1	0.60			198
Total		88		336		46		7		2		479
Percentage		18.37		70.15		9.60		1.46		0.42		

The figures in table 10, when compared with those in table 9, clearly show that the results obtained by the examination of the ripe fruits are practically the same as those secured by the examination of picked flowers. It is true that the range of the variation determined by the former method is somewhat limited owing to the failure of the flowers with high numbers of carpels to set fruits, but the percentage ratio between the normal and all abnormal flowers—17.98 : 82.02—is practically the same as the percentage ratio between the normal and all abnormal fruits 18.37 : 81.63.

Turning to the question of the behavior of the offspring from normal and abnormal fruits borne by the same plant we may now consider the results obtained for the plants in pots 36, 37 and 38. The data on the plants of the last-named pot have not been included in table 9, as they were not collected daily as in the case of the plants in the other pots. As will be remembered the plants in pot 38 originated from three-angular

fruits, those in pot 37 from four-angular, and those in pot 36 from five-angular fruits. The data on the offspring of the four- and five-angular fruits have been already given in tables 9 and 10, pots 36 and 37, respectively. The data on the 3 plants that had originated from triangular fruits in pot 38 are given in table 11.

TABLE 11

Number of carpels	3	4	5	6	7	9	10	12	16	Synanthies
Number of flowers	64	226	27	7	3	3	1	3	2	8
Percent	18.60	65.71	7.85	2.03	0.87	0.87	0.29	0.87	0.58	2.33

The examination of the fruits of 11 plants that had originated from three-angled fruits and grown in pot 38 along with the three plants just dealt with, gave the following result: 15.32 percent of three-angular fruits, 76.64 percent of four-angular, 6.57 percent of five-angular, 0.73 percent of six-angular fruits, and 0.73 percent of syncarpous fruits.

From a comparison of the figures just given with those in table 9 for the plants in pots 36 and 37, it is evident that the offspring raised from three-angular fruits reproduce the same type and scope of variability as the offspring raised from abnormal, four- or five-angular fruits. The similarity of conditions prevailing in all the three progenies is brought out more plainly by bringing together their respective percentage ratios between the normal and abnormal flowers or fruits (see table 12).

TABLE 12

	No. of plants	Angles of fruits planted	Percentage yields of fruits	
			Normal	Abnormal
Pot 38	3	3	18.60	81.40 (flowers)
	11	3	15.32	84.68 (fruits)
Pot 37	3	4	19.05	80.95 (flowers)
	7	4	17.60	82.40 (fruits)
Pot 36	3	5	17.36	82.64 (flowers)
	7	5	23.02	76.98 (fruits)

From a morphogenetic point of view these results in conjunction with the other similar data collected on the previous generations, are of importance. They indicate that the descendants of this race reproduce the ever-sporting type of the mother plant regardless of whether they

originated from normal or abnormal fruits of the parent. This is in accord with the observations of DE VRIES (1910, p. 526) on fasciated races and other ever-sporting varieties, and of BATESON and MISS PERTZ (1900) on *Veronica Buxbaumii*. The normal three-carpelled flower or the triangular fruit of the ever-sporting variety represents only apparent (phenotypic) reversions to the original, normal type of the species; in reality they carry the potentialities of the ever-sporting character which their offspring manifest in practically the same degree as the progeny raised from the abnormal fruits of the race.

This dimorphism is a typical attribute of this ever-sporting line and as constant as the monomorphic, normal type is characteristic of line No. 22. This is demonstrated by the following experiment. As will be remembered line No. 22 produces under favorable conditions as high as 5 percent of four-angular fruits, the remaining being triangular. As soon as the type of this line had been established it became a matter of interest to find out the behavior of the offspring raised from four-angular fruits borne by plants of this strain. In this experiment four-angular fruits of a fourth-generation plant that had developed 97.28 percent of three-carpelled and 2.72 percent four-carpelled flowers, were planted in the summer of 1918, in pot 69 which was filled with rich, fertilized soil and placed in the greenhouse at the AROOSTOOK FARM. As a check triangular fruits of the same plant were planted in pot 51 under the same conditions of environment. From the four-angular fruits only one plant was raised to maturity which yielded 662, or 97.35 percent, of triangular fruits and 18, or 2.65 percent, of four-angular fruits. The two plants that were raised as a check from triangular fruits of the same mother plant yielded 749 or 97.53 percent of triangular fruits, 18 or 2.34 percent of four-angular, and 1 five-angular fruit. These results clearly show that the four-angular fruits which only rarely occur on plants of line 22 reproduce the normal monomorphic type of that line in a degree almost identical with that produced by the triangular fruits of that race.

We may now turn to the variations of the perigone in the fourth-generation plants. The data dealing with this phenomenon are more exhaustive than those for the first generation. They were recorded for the plants in pots 36, 37 and 39, daily, on the same flowers that were discussed above with respect to variations in the gynoecium. The actual distribution of the flowers with regard to the number of leaves in the perigone and the percentage frequencies for each category of flowers of each plant as well as the percentage frequencies for the total number of flowers are given in table 13.

TABLE 13

LINE NO. 5.—*Actual* (f) *and percentage frequencies of number of flowers with respect to number of perigone leaves.*

Plant No.	Number of perigone leaves																Total
	5		6		7		8		9		10		11		12		
	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	
Pot No. 36 1	308	70.32	105	23.97	18	4.11	1	0.91	2	0.46	1	0.23					438
Pot No. 36 2	214	64.65	89	26.89	21	6.34	5	1.51	1	0.30	1	0.30					331
Pot No. 36 3	410	69.97	141	24.06	23	3.92	7	1.19	3	0.51	2	0.34					586
Pot No. 37 4	541	70.90	162	21.23	37	4.85	14	1.83	1	0.13	7	0.92			1	0.13	763
Pot No. 37 5	447	69.63	150	23.86	29	4.52	11	1.71			5	0.78					642
Pot No. 37 6	538	76.31	131	18.58	28	3.98	5	0.71	2	0.28	1	0.14					705
Pot No. 39 7	604	72.86	169	20.39	31	3.74	13	1.57	7	0.84	5	0.60					829
Pot No. 39 8	784	73.41	212	19.85	44	4.12	10	0.94	4	0.37	10	0.94	1	0.09	3	0.28	1068
Total	3846		1159		231		69		20		32		1		4		5362
Percentage	71.72		21.62		4.31		1.29		0.37		0.59		0.02		0.08		

As in the case of the first generation the number of flowers with a normal five-parted perigone is far in excess of the number of flowers with abnormal perigones. The variation is unilateral, the frequencies decreasing as the number of perigone leaves increases. The ratio between the normal and abnormal perigones in the fourth-generation plants is more in favor of the abnormal perigones than in the first-generation plants, owing, undoubtedly, to the fact that in the former case the observations on the variations of the perigone were complete while in the latter case they have not been recorded for a number of flowers.

In examining the flowers it was noted that the variations in the gynoecium were associated with abnormalities in the perigone. This relation is illustrated in table 14.

TABLE 14

LINE NO. 5.—*Actual frequencies showing relation between number of carpels and number of perigone leaves.*

Number of perigone leaves	Number of carpels																Total
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
5	878	2629	250	33	19	20	13	15	1	9	1	—	—	—	—	—	—	3868
6	86	934	105	25	1	7	1	—	—	—	—	—	—	—	—	—	—	1159
7	13	114	60	22	4	—	—	—	—	1	—	—	—	—	—	—	—	214
8	2	10	8	10	5	15	1	10	1	—	1	1	—	—	—	—	—	64
9	—	—	1	3	6	1	5	3	1	—	—	—	—	—	—	—	1	21
10	—	—	—	—	—	4	7	11	1	5	1	1	—	—	—	—	—	30
11	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1
12	—	—	—	—	—	—	—	1	—	1	—	1	—	—	—	1	—	4
Total	979	3687	424	93	35	47	27	41	4	16	3	3	—	—	—	1	1	5362

In this table are presented the actual frequency distributions in relation to the number of carpels and perigone leaves. This relation is more clearly brought out by the percentage frequencies given in table 15.

From tables 14 and 15 it is evident that the variations in the gynoecium are correlated with the abnormalities in the perigone. The normal, three-carpelled flowers show the highest percentage of normal five-parted perigones. In the same measure as the number of carpels increases, the frequency of normal, five-parted perigones, on the whole, decreases, the normal perigone being substituted by those with a higher number of leaves. Thus, perigones with 9 leaves and above are not associated with three-carpelled or even four-carpelled gynoecia, while gynoecia with a number of carpels above 13 are not found to be associated with five-, six-, or seven-parted perigones.

TABLE 15

LINE No. 5.—*Percentage frequencies showing relation between number of carpels and number of perigone leaves.*

Number of perigone leaves	Number of carpels													
	3	4	5	6	7	8	9	10	11	12	13	14	18	19
5	89.68	71.30	58.96	35.48	54.29	42.35	48.15	36.59	25.00	56.25	33.33			
6	8.78	25.33	24.76	26.88	2.85	14.89	3.70							
7	1.33	3.09	14.15	23.66	11.43					6.25				
8	0.20	0.27	1.88	10.75	14.29	31.91	3.70	24.39	25.00		33.33	33.33		
9			0.24	3.23	17.14	2.13	18.52	7.32	25.00					100
10						8.51	25.93	26.83	25.00	31.25	33.33	33.33		
11								2.44						
12								2.44		6.25		33.33	100	
Total	99.99	99.99	99.99	100.00	100.00	99.99	100.00	100.01	100.00	100.00	99.99	99.99	100	100

This correlation between the number of carpels and the number of perigone leaves will be recurred to in the discussion of the periodicity in the occurrence of the abnormalities in this race.

The behavior of the fourth generation of line No. 22 may be briefly mentioned here. Triangular fruits from a third-generation plant that had grown in the garden in the preceding summer, were planted in pot No. 46 filled with composted soil and placed in the UNIVERSITY greenhouse along with the plants in pots Nos. 36-39, considered above. Three plants whose flowers were examined, yielded 578 or 97.28 percent three-carpelled and 11 or 2.72 percent four-carpelled flowers. These results show a rather lower degree of variability than in the first generation of this line. Compared, however, with the second and third generation of this race, the fourth generation is appreciably more variable.

Fifth generation

The fifth generation of these two strains was grown in the open garden and in the greenhouse at AROOSTOOK FARM in the summer of 1918. This generation has again borne out the constancy of the type of variability of the two lines under a given set of environmental conditions. The series of plants of line No. 5 grown in the greenhouse yielded data given in table 16.

TABLE 16

	Number of fruit-angles				
	3	4	5	6	7
Percentage frequency	34.58	49.40	15.33	0.51	0.17

The fifth-generation plants of this race grown in the garden made a very vigorous growth, as each plant was allowed ample space, 2 feet square, to stimulate the development of fasciations. The mode of variations in the gynoecium, however, did not deviate materially from the third generation grown in the open in 1917. The examination of these plants gave the percentage frequencies shown in table 17.

TABLE 17

	Number of fruit-angles					
	3	4	5	6	7	8
Percentage frequency ...	50.78	44.47	4.16	0.37	—	0.21

The fifth-generation plants of line No. 22 in the greenhouse yielded 97.35 percent of three-angled and 2.65 percent of four-angled fruits.

The analysis of the five generations of the two strains of *Fagopyrum tataricum* has brought out the following points. The ever-sporting strain, after isolation, at once displayed the highest degree and fullest scope of its variability reached in the subsequent generations under similar conditions. The ever-sporting character was transmitted to all members of subsequent generations with a striking regularity and uniformity in its degree and scope under a given set of conditions of environment. The extent of the reversion of the ever-sporting character towards the normal specific type as evidenced by the lower proportions of abnormal forms in certain generations, was proved to be controlled by the environment since upon bringing up the subsequent generation under the original conditions, the original degree and range of variability was restored. Selection appeared to have no effect whatever upon the improvement of the ever-sporting variety. The effect of nutrition will be considered in a later section of this paper.

PERIODICITY IN THE MANIFESTATION OF THE CHARACTERS OF THE EVER-SPORTING VARIETY

DE VRIES (1905, p. 361, 1910, p. 323) has established for a number of ever-sporting varieties that the occurrence of their abnormalities is subject to a definite law. According to his observations this law is determined by the individual strength of the different organs of the ever-sporting plant which in turn is determined by external conditions of life, primarily nutrition. "The stronger a bud is the more it is liable to produce anomalies" (DE VRIES 1910, p. 324). This would explain the more frequent occurrence of abnormalities in best nourished regions

on the plant so frequently observed in many instances by DE VRIES. In its application to the plant as a whole this law represents an instance of the fundamental rule that every living organism shows in the course of its life a gradual increase in strength to a maximum after which a decline in vigor follows. DE VRIES sees a rhythmic parallel between this general law of periodicity in the life cycle of a plant and the manifestation of anomalies, the height of the development and differentiation of the plant coinciding with the maximum output of abnormalities. This would explain the periodical occurrence of abnormalities at different periods of the life cycle of the plant, as illustrated by numerous examples cited by DE VRIES. According to these considerations the operation of the law of periodicity can be briefly defined by stating that it manifests itself in two ways: in determining the occurrence of abnormalities in relation to position on the different parts of the plant, and in relation to time in the cycle of the plant life.

Apart from DE VRIES's numerous observations many of which, however, are of a casual nature, the validity of this law has been critically tested in only a few instances. BATESON and PERTZ (1900, p. 82) found that the "chief output of abnormal flowers of *Veronica Buxbaumii* takes place in the earlier part of the flowering season, and especially just before the greatest output of flowers, after which time the percentage of abnormality declines." HERIBERT-NILSSON (1912, p. 112) states that the number of flowers with supernumerary stigmas in *Oenothera Lamarckiana* decreases toward the end of the flowering season. TINE TAMMES (1904) in her study on the occurrence of abnormal leaves in *Trifolium pratense quinquefolium* found that the distribution upon the plant of each of the two anomalies, the lateral and terminal doubling of the leaves, is subject to a definite law according to which the maximum output of leaves laterally doubled occurs on the lower part of the primary axis while the terminally doubled leaves occur more frequently in the vicinity of the inflorescence. But as the absolute number of laterally doubled leaves is far in excess of the absolute output of terminally doubled leaves, TAMMES found that young plants of the "five-leaved" clover show higher proportions of abnormal leaves than the fully grown plants. Here, then, are introduced, for the first time, two abnormal characters on the same plant into the study of the behavior of abnormalities, and we note that the maximum output of each of the abnormalities is confined to different parts of the plant. A further instance of the study on the occurrence of two abnormalities on the same plant is

furnished by LEHMAN (1909) in his account of variations in *Veronica agrestis*. He found for *Veronica Tournefortii* that the time of the maximum production of abnormal calyces does not coincide with the period of the maximum output of abnormal corollas with the doubled anterior petals on the same plant. From this he concludes that nutrition does not determine the periodicity in the occurrence of abnormalities.

The studies of TAMMES and LEHMAN would seem to demonstrate the desirability of subjecting the entire period of occurrence of abnormalities to a statistical examination before any definite picture of the actual type of variation of an ever-sporting variety can be drawn. Furthermore, the exact determination of the distribution of the anomalies upon the different parts of the plant may also have a possible bearing upon the study of the effect of nutrition, or starvation upon the manifestation of abnormal characters. If, for example, the maximum output of abnormal flowers of a certain strain occurs on the most differentiated parts of the plant it is clear that scant nourishment will reduce the volume of differentiation and with it also the number of abnormal flowers. But this reduction cannot be ascribed to unfavorable conditions having a direct effect upon the inherent tendency to vary. It is simply due to the lack of the most favorable region for its expression that this tendency appears weakened.

Frequency distribution of different types of flowers with regard to position on the plant

All these considerations made it appear desirable to study the manner in which the abnormal flowers of this race occur on the different parts of the plant and at different periods of the flowering season. The material for this study comprised the fourth-generation plants grown in the UNIVERSITY greenhouse in the winter of 1918, and was so selected as to include progenies of the same plant but originated from different forms of abnormal fruits. Accordingly, 3 plants in pot 36 raised from five-angled fruits were selected for this purpose. The medium in both these pots consisted of ordinary garden soil. In order to determine any possible effect of high nutrition upon the distribution of flowers, 2 plants raised from four-angled fruits but grown in rich, composted soil, were included in the material. We are already familiar with the total number of flowers and the different categories, of these 8 plants as they have been discussed above as representatives of the fourth generation of the ever-sporting race (see table 9).

The distribution of flowers at different periods of the flowering season and on the different parts of the plants was determined by daily picking and examining the flowers as they appeared on the plants. The flowers were daily recorded according to a scheme that permitted the construction of a mental picture of the whole plant and the tracing of each flower to its original position on the plant after all the flowers had been recorded. A few remarks regarding the essential morphological features of our plants will serve to elucidate this scheme as well as the analysis of the collected data.

Under the conditions prevailing in the greenhouse of the UNIVERSITY at Orono the plants (figures 8.and 9) reached an average height of 22 cm. They developed a main stem or primary axis bearing 7, in a few cases 6, alternate leaves. Only the first three buds in the axils of the first three leaves from below developed secondary branching axes which usually bore 3-4 leaves. The buds in the axils of the first, second and seldom the third leaf on the secondary branch developed two, rarely three tertiary branches. The last, 3rd or 4th, leaf on these always subtended the terminal raceme. The flowers produced in the axils of leaves on the secondary and tertiary branches were borne on short peduncles. With the production of the tertiary branches the branching of the plant was concluded. The upper leaves on the main stem, from the fourth leaf on, did not develop branches, the buds in their axils giving rise only to peduncles bearing racemes. From the third leaf on, the main stem gradually grew weaker, tapering upward and ultimately going over into a slender raceme subtended by the last, usually seventh, leaf. An abnormal feature of the plants of line No. 5 was the production of short, proliferating shoots in the axils of the cotyledons.

In daily recording the flowers the position of each flower was first noted in relation to the leaves (Phyl) on the main stem or primary axis, that is to say, whether the flower was located on one of the three secondary branches or one of the raceme-bearing peduncles in the axils of the 4th to the 7th leaves. After this general orientation the position of the flower was further determined in relation to the component parts of the secondary system of branching or to the different regions on the axis of inflorescences of the racemes in the axils of the 4th to 7th leaves. A concrete example may illustrate this method of recording the flowers $Phyl_2R_2l_3$ designated a flower located in the axil of the third leaf (l_3) borne by the right secondary axis (R_2) which had originated in the axil of the second leaf ($Phyl_2$) on the main stem; $Phyl_3L_3r_2l_1$

indicated a flower located in the axil of the first leaf borne by the second right tertiary branch (r_2) that had sprung from the axil of the second leaf of the third left secondary branch (L_3) that had originated in the axil of the third leaf ($Phyl_3$) on the main stem. By the use of this method the original position of each flower on the plant could be determined.

Let us now consider first the frequency distribution of flowers with regard to the position on the plant, i.e., whether any form of flowers is produced with any greater frequency in certain regions of the plant than in others. In order to obtain a general information regarding this question the daily recorded data were first grouped so as to give the actual and relative output of each kind of flowers produced by each organ of the plant, as a whole, originated in the axils of each of the 7 leaves on the main stem. In table 18 are given the actual and percentage frequencies of the flowers for each of the organs sprung from the axillary buds on the main stem. These data represent summarized results taken from tables prepared for each plant separately. The first horizontal row gives the flowers borne in the axils of the cotyledons.

From an examination of this table the following points are evident. The percentage frequencies of the normal three-carpelled flowers show a fairly marked uniformity for each of the different organs of each plant. These frequencies approach very well the percentage frequency of normal flowers in all the 8 plants as a whole, which is 17.98 (see table 9). From the fact that the percentage ratios between the normal and abnormal flowers of each plant organ are markedly uniform it may be concluded that the causes that govern the percentage ratios between the normal and abnormal flowers for the whole plant obtain also with marked regularity in each individual organ of the plant.

With regard to the range of variability or its intensity, as measured by the frequency occurrence of the most aberrant variants we may clearly discern in table 18 that there are regions on the plant that show a wider scope of variability than others. The first two branches, and especially the second one, that yielded the highest output of flowers, mark also the place of greatest variability on the plant as evinced by the great amplitude of aberrant flower forms including the greatest number of synanthous flowers. The synanthous flowers borne by the racemes in the axils of the 4-7 leaves were all contributed solely by the plants in pot 36 which were raised from five-angled fruits. This may indicate a slightly greater intensity in the variability of plants originated from

TABLE 18

LINE NO. 5.—*Actual (f) and percentage frequency distribution of flowers borne by each organ of each plant, with respect to number of carpels.*

Position of flowers	Number of carpels																														Synanthies		Total
	3		4		5		6		7		8		9		10		11		12		13		14		16		18		19				
	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent	f	percent		
Cotyledons	97	16.33	389	65.71	60	10.14	15	2.53	3	0.51	5	0.84	3	0.58	4	0.68	1	0.17	5	0.84					1	0.17					9	1.52	592
Branch 1	334	18.75	829	66.43	105	8.41	21	1.68	8	0.64	10	1.52	6	0.48	12	0.96											1	0.08			13	1.04	1248
Branch 2	245	18.39	880	66.07	98	7.36	25	1.88	14	1.05	8	0.60	4	0.30	15	1.13	2	0.15	5	0.38	3	0.15	2	0.15					1	0.15	31	2.33	1332
Branch 3	242	17.60	927	67.42	111	8.07	23	1.82	8	0.58	13	0.95	13	0.95	7	0.51	1	0.07	6	0.44	1	0.07									21	1.53	1375
Raceme in axil of leaf 4	37	16.30	167	73.57	15	6.61	2	0.88	1	0.44					2	0.88							1	0.44							2	0.88	227
Raceme in axil of leaf 5	20	15.75	93	73.23	11	8.66	1	0.78																							2	1.57	127
Raceme in axil of leaf 6	38	19.10	144	72.36	11	5.93	2	1.01	1	0.50					1	0.50															2	1.01	199
Terminal raceme above leaf 7	66	19.19	258	75.00	13	3.72	2	0.58			2	0.58	1	0.29																	2	0.58	344
Total	979		3687		424		93		35		47		27		41		4		16		3		3		1		1		1		82		5444

TABLE 19

LINE NO. 5.—*Frequency distribution of number of flowers per each organ of the secondary branches alone, in all plants.*

Position of flower	Number of carpels												Percentage ratio between normal and abnormal flowers
	3	4	5	6	7	8	9	10	12	19	Synanthies	Total	
In axil of l_1	6	16	2									24	25.00 : 75.00
In axil of l_2	8	46	13	5		2	1				1	76	10.53 : 89.47
In axil of l_3	26	91	14	4	3			2			1	141	18.44 : 81.56
In axil of l_4	16	61	4	1	1				1			84	19.05 : 80.95
At base of raceme (ba.)	35	141	12	4	4	1		3		1	11	215	16.28 : 83.72
At apex of raceme (ctr. tr.)	112	303	36	5	4	2	3	2	1		6	474	23.63 : 76.37
Total	203	661	81	19	12	5	4	7	2	1	19	1014	20.02 : 79.98
Percentage	20.02	65.19	7.99	1.87	1.18	0.49	0.39	0.69	0.20	0.10	1.88		

TABLE 20

LINE NO. 5.—*Frequency distribution of number of flowers per each organ of each of the tertiary branches, in all plants.*

Position of flower	Number of carpels												Synanthies	Total	Percentage ratio between normal and abnormal flowers
	3	4	5	6	7	8	9	10	11	12	13	18			
In axil of l_1	27	78	11	4									3	123	21.25 : 78.05
In axil of l_2	16	77	9	2	1	2	2	3	1	1	2		4	120	13.33 : 86.67
At base of raceme (ba.)	22	85	23	3		2	3			1		1	5	145	15.17 : 84.83
At apex of raceme (ctr. tr.)	61	192	16	2		3	1	4			1		5	285	21.40 : 78.60
Total	126	432	59	11	1	7	6	7	1	2	3	1	17	673	18.72 : 81.28
Percentage	18.72	64.19	8.77	1.65	0.15	1.04	0.91	1.04	0.15	0.30	0.45	0.15	2.53		

five-angled fruits than in those from three- or four-angled fruits, a condition not infrequently observed in this race.

From table 18 it is further to be noted that the range of variability shown by the flowers borne by the racemes in the axils of the 4-7 leaves is very limited as is also the actual number of flowers. From the totals in the last vertical row in table 18 we note the yielding capacity of each plant organ. The three branches in the axils of the three lowest leaves yielded the highest output of flowers; the cotyledonary organs range next, to be followed by the terminal raceme and the racemes in the axils of the 4th leaf on the main stem; the racemes in the axils of the fifth and sixth leaves yielded the lowest number of flowers. From these data we may conclude that the yield of Tartary buckwheat plants is determined, broadly speaking, by the basal regions of the plant. This fact is of importance in relation to the aims of practical breeding, and suggests the desirability of adopting such cultural methods as would favor the development and differentiation of the lower plant body rather than the extension of the upper part at the expense of basal differentiation.

Table 18 gives the general distribution of flowers upon the different plant organs taken as a whole. We may now analyze these organs into their differentiated components. Four plants, No. 5, 6, 7 and 8, were selected for this analysis. As already noted, only the three lowest axillary buds on the main stem gave rise to differentiated branching organs, each producing 2-3 tertiary branches. In table 19 is given the frequency distribution of flowers upon the secondary branches alone, excluding the tertiary ones. The flowers are grouped here in six categories. In the first four classes are grouped the flowers that were borne in the axils of the 1st-4th leaves (l_1, l_2, l_3, l_4) on each of the secondary branches. The last two categories include flowers borne exclusively by the terminal raceme of each secondary branch. On these terminal racemes the flowers were recorded for three regions of the axis of inflorescence: The flowers in the basal region of the axis of inflorescence (bs.) the terminal flowers (tr.) and those immediately below and close to them (ctr.). The flowers recorded for the last two regions are grouped in one class in table 19 (ctr., tr.).

In table 20 is presented the frequency distribution of flowers upon the tertiary branches.

Both tables 19 and 20 represent summarized results taken from tables made out for each plant separately. A comparison of the data given in both tables shows that the distribution of flowers upon the

secondary and tertiary branches have certain points in common, though an absolute comparison is not permissible since the tertiary branches did not develop the third and fourth leaf. From the totals for each component of the secondary and tertiary branches it will be noted that the highest output of flowers was produced in the apical region of the terminal raceme and the next highest in the basal zone of the axis of inflorescence. If the production of synanthous flowers is indicative of a high tendency to vary and proliferate it would point to the basal region of the terminal raceme as the seat of greatest variability. This is brought out by tabulating the percentage frequencies of synanthous flowers for each organ of each branch system as illustrated in table 21.

TABLE 21
Synanthous flowers in percent.

Position of flower	Secondary branch	Tertiary branch
l_1		2.44
l_2	1.33	3.33
l_3	0.71	
l_4		
bs.	5.16	3.45
ctr. tr.	1.26	1.75

From tables 19 and 20 it will further be noted that while the percentage ratio between the total number of normal and abnormal flowers of the secondary and tertiary branch, respectively, very well agrees with that for the plants as a whole, the percentage ratio between the normal and abnormal flowers for each individual organ of both branching systems shows a considerable deviation from the average percentage for the whole branching system. In spite of the relatively small number of flowers involved these deviations are undoubtedly significant since the corresponding homologous component elements of the secondary and tertiary systems show an analogous rise and drop in the proportion of normal flowers. This may be seen from the last vertical columns in tables 19 and 20. Thus the axillary buds of the first leaves favor the production of normal flowers, 25 percent and 21.95 percent, respectively; the buds in the axils of the second leaves appear to produce the lowest percentage of normal flowers, 10.53 percent on the secondary branch and 13.33 percent on the tertiary branch. The axillary buds of the 3rd and 4th leaves on the secondary branch produce the average proportion of normal flowers, while at the base of the terminal racemes the propor-

TABLE 22

LINE NO. 5.—*Percentage frequencies of number of flowers with respect to number of carpels for successive periods of 7 days.*

Date	Number of carpels														Synanthies	Total	Percentage ratio between normal and abnormal flowers
	3	4	5	6	7	8	9	10	11	12	13	14	18	19			
March 6-12.....	27.85	54.38	13.38	1.86	0.27	0.79		0.53							0.79	100.00	27.85 : 72.15
March 13-19.....	23.17	67.56	5.85	0.73	0.49	0.24		0.73		0.24					0.98	99.99	23.17 : 76.83
March 20-26.....	15.06	72.81	5.17	2.25	0.89	0.22		0.45			0.22				2.92	99.99	15.06 : 84.94
March 27-April 2	14.56	66.84	7.72	3.68	0.88	1.40	0.53	1.40		0.18		0.18			2.63	100.00	14.56 : 85.44
April 3-9.....	19.31	65.15	8.95	1.26	0.78	0.94	0.47	0.31		0.47			0.16		2.20	100.00	19.31 : 80.69
April 10-16.....	11.74	71.68	8.12	2.07	0.52	1.55	0.69	1.03		0.17		0.17			2.25	99.99	11.74 : 88.26
April 17-23.....	18.65	70.68	4.81	0.90	0.60	0.90	0.60	0.60	0.45	0.30	0.15			0.15	1.20	99.99	18.65 : 81.35
April 24-28.....	20.72	68.63	6.27	0.76	0.76		0.38	1.14				0.19			1.14	99.99	20.72 : 79.28

TABLE 23

LINE NO. 5.—*Percentage frequencies of number of flowers with respect to number of perigone leaves for successive periods of 7 days.*

Date	Number of perigone leaves										Total	Percentage ratio between normal and abnormal flowers
	5	6	7	8	9	10	11	12	13	14		
March 6-12.....	81.96	14.59	1.85	1.06	0.27	0.27					100.00	81.96 : 18.04
March 13-19.....	80.00	15.12	2.93	0.49	0.49	0.24	0.24	0.49			100.00	80.00 : 20.00
March 20-26.....	60.67	28.09	6.74	1.57	0.45	1.35	0.22	0.90			99.99	60.67 : 39.33
March 27-April 2.	72.63	19.65	4.21	1.75	0.35	1.05	0.18	0.18			100.00	72.63 : 27.37
April 3-9.....	71.90	19.62	5.48	1.11	0.47	0.78		0.63			99.99	71.90 : 28.10
April 10-16.....	71.50	21.93	4.15	1.04	0.35	0.86		0.17			100.00	71.50 : 28.50
April 17-23.....	63.46	28.87	3.01	1.35	0.90	1.05		0.30	0.15		99.99	63.46 : 36.54
April 24-28.....	64.64	28.71	2.85	1.90	0.38	1.14		0.19		0.19	100.00	64.64 : 35.36

tion of normal flowers drops to finally increase again above the average in the apical region of the racemes.

From the data presented in tables 18-20 the following conclusions may be drawn with reference to the distribution of flowers upon the plants of this race. The greatest output of flowers was produced in the lower, differentiated parts of the plant. The ratio between the normal and abnormal flowers appears fairly uniform under the prevailing conditions of environment, for each of the collective plant organs arisen from the axillary buds on the main stem. The analysis of the collective organs into their component parts reveals a marked variation in the percentage frequencies of normal and abnormal flowers produced by the axillary and terminal buds on the secondary and tertiary branches, the axillary buds of the second leaf and the basal zone of the terminal raceme producing the highest relative number of abnormal flowers. Relative to the range or intensity of variability it is again the lower, most differentiated parts of the plants, more specifically the component parts of the second and third secondary branch, especially the former, that exhibit the widest amplitude of aberrant flower forms. To specify it more closely, the basal regions of the terminal raceme of the secondary and tertiary branches are the seat of the greatest tendency to proliferate as evinced by the wide range of aberrant forms. This is in accord with the observations of DE VRIES (1910, p. 329) who found the lower end of many racemose inflorescences to be a place specially favorable to anomalies.

FREQUENCY OF OCCURRENCE OF DIFFERENT TYPES OF FLOWERS IN RELATION TO DIFFERENT PERIODS OF THE FLOWERING SEASON

Having considered the distribution of flowers with reference to their position on the plant body, we may next inquire into the frequency of occurrence of the different flowers in relation to the different periods of the flowering season. For this purpose the daily recorded data were brought together into 8 groups, each (except the last one) covering a successive flowering period of 7 days, and all making up the entire flowering season during which 5444 flowers were recorded.

In table 22 are given the percentage frequencies of the flowers with respect to number of carpels computed on the basis of actual frequencies noted for each successive week.

From the data presented in table 22, it is evident that the first two weeks of the flowering season mark the lowest relative production of abnormal flowers. From the second week the relative total number of

abnormal flowers increases to reach a maximum in the third and fourth week. In the course of the fifth week, April 3-9, the proportion of abnormal flowers drops markedly to reach another more distinct maximum in the sixth week. The last two weeks of the flowering season again mark a slow decrease in the relative production of abnormal flowers.

The rather striking depression in the relative production of abnormalities in the gynoecium in the course of the fifth week is of interest. That this depression is significant is shown by the figures given in table 23, which indicate that at about the same period a similar reduction occurred in the relative output of abnormalities in the perigone, which, as will be recollected (see table 15) are associated with abnormal gynoecia.

From table 23 it will be noted that also in the case of the perigone variations the first two weeks mark the lowest relative production of abnormal perigones. The maximum was reached in the course of the third week, after which, in close analogy to the variations in the gynoecium, a depression followed, which, however, in this case extended over a period of three weeks when the abnormalities again increased..

The similarity of effect upon both kinds of abnormalities would point to a common cause which in the case of the perigone variations was more effective than in the variations of the gynoecium. The nature of this cause may have been internal or external. About the fourth week of the flowering season, the plants, owing to the continuous removal of their flowers, gave rise to abnormal growth by producing several short shoots in the axils of the cotyledons bearing numerous flowers. It is conceivable that this abnormal vegetative growth may have caused a disturbance in the function of the specific determiners conditioning the manifestation of abnormal flowers. A more plausible explanation, however, may be found in external influences of environment. The plants of the race used in this investigation grew along with a host of other plants that were frequently watered; this caused the air to be very moist and damp. During the first week of April, owing to the illness of the man in charge of the greenhouse, the plants were not watered frequently, with the result that the air in the greenhouse during that period was very dry. The concurrence of this period of dryness with the reduced output of abnormal flowers would point to moisture as the factor of environment facilitating the realization of the abnormal flowers in this race. This was also borne out by results obtained from cultures grown under different conditions of environment, though further and special experiments are yet required to obtain conclusive evidence on this question.

Neglecting for a moment the above disturbance in the floral variations we may conclude from an inspection of the data given in the last vertical rows in tables 22 and 23, that under the prevailing conditions the first and second week of the flowering season mark the lowest relative production of abnormal flowers, after which a marked and sudden increase in the output of abnormalities ensues. To that extent our data are in accord with the observations of DE VRIES. But the behavior towards the end of the flowering season, which is marked by only a small decrease in the percentage of abnormalities, does not conform to the rule established by DE VRIES, according to which the relative output of abnormality shows a rapid and marked decline towards the final period of the flowering season. This behavior of our race was found to be due to the manner in which different flowers are distributed upon the different parts of the plant. As it will be recollected (see table 18) the racemes borne in the axils of the 4th-7th leaves show the narrowest range of variability. Now, it is just this section of the plant, from the fourth leaf up, that contributes the bulk of flowers during the first two weeks of the flowering season. During the following weeks the differentiated organs of the lower section of the plants, the secondary and tertiary branches, come into play, raising very markedly the percentage of abnormal flowers since these differentiated branches, as will be remembered, are the very seat of greatest intensity of variation. Towards the end of the flowering season the upper regions of the plants produce only very few flowers while the lower-differentiated parts sustain their flower production to the end of the flowering season. This differential distribution of flowers upon the parts of the plant and the sequence in the unfolding of the flowers explains the relationship, referred to above, between the normal and abnormal flowers during the different periods of the flowering season: the plants begin flowering in the region marked by a narrow range of variability and finish in the regions of greatest intensity of abnormal development.

In considering the periodicity in the distribution of normal and abnormal flowers of this race it should be borne in mind that the plants used in this investigation were grown in the greenhouse and under conditions manifestly favoring the development of abnormalities. It is quite possible that the conditions prevailing in the open might operate in a different manner upon the manifestation of abnormality than in the greenhouse. With this reservation in mind, we may state that the examination of the distribution of the flowers upon the different parts of

the individual plant points, in conformity with the observations of DE VRIES and other writers, to the existence of a specific region on the plant in which the tendency to vary and to proliferate is most pronounced. Contingent upon this distribution with respect to position on the plant, and, indeed, a function of it, is—barring external interference—the varying percentage ratio between the normal and abnormal flowers in the successive periods of the flowering season.

FASCIATION IN *Fagopyrum tataricum*

A further teratological feature exhibited by this race is fasciation. The writer is aware of no previous record of fasciation in *Fagopyrum tataricum*.

Fasciation was first observed on plants of the fourth generation grown in the UNIVERSITY greenhouse in 1918, the variations of which have been the subject of the discussion in the preceding section. Fasciated branches were found on plant 8 growing in pot No. 36 and on plant 6 and 5 in pots 37 and 39 respectively. It should be stated that three of these four plants have not been included in the study of periodicity and, consequently, were not subjected to any possible traumatic influence entailed by the daily removal of flowers.

The first indication of a fasciated condition was noted in the altered phyllotaxy. The leaves at the first node on the main axis were inserted opposite each other instead of the normal alternate insertion. The branch that sprung from their axillary bud presented a flattened ribbon-like condition with a distinct groove running up to the summit at which point the branch resolved itself into two subdivisions each bearing a raceme. As the plants were small (about 25 cm tall) and fairly crowded in the pots the fasciations were not very conspicuous. It was not until the summer of 1918 that beautiful specimens of fasciations were obtained among the cultures grown in the garden. In order to stimulate the development of fasciations by abundant nutrition, the fruits from plants in the pots Nos. 36-39 as well as from some other plants of this race were planted out 2 feet apart each way. The plants made a very vigorous and luxuriant growth developing strong primary and secondary branches. It was the latter system of branches and among these usually the lower ones, at the first node above the cotyledons, that presented the best specimens of fasciation.

The morphological aspect of these fasciations was generally similar to that recorded in other genera. The fasciated branches often presented

below a nearly cylindrical form, which in the upper part changed into a flattened condition, and ultimately, at one of the nodes split into two or more branches of more or less normal aspect. Such a case is illustrated in figure 5. From this figure the altered arrangements of the

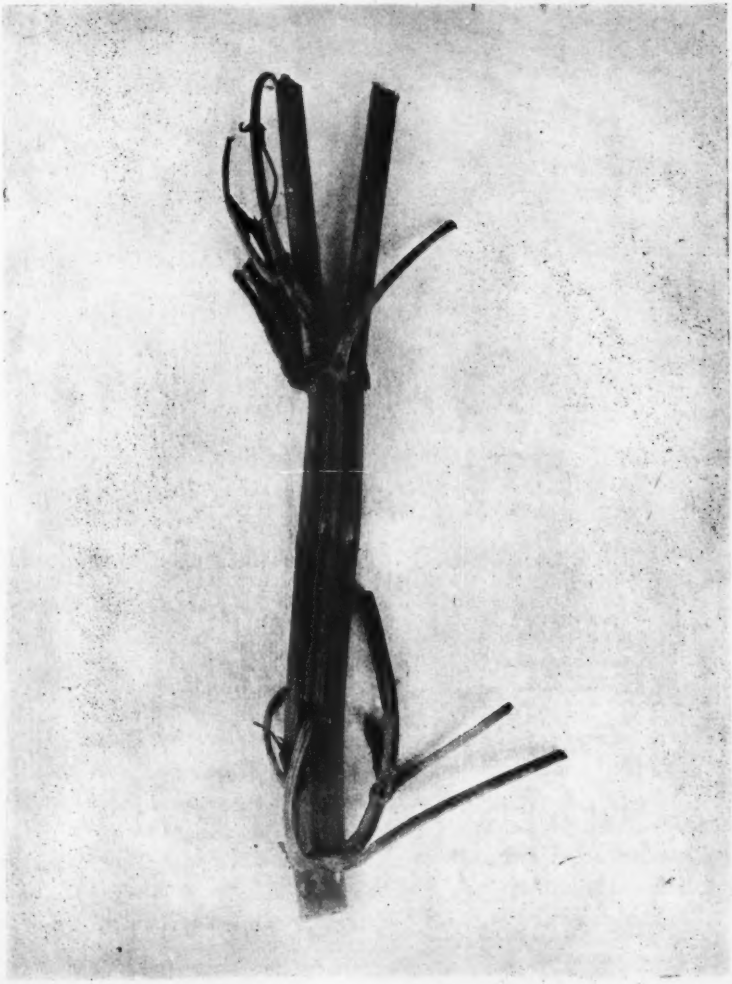

FIGURE 5.—Fasciation in *Fagopyrum tataricum*. A fasciated branch showing altered phyllotaxy and splitting of branch at node into 2 subdivisions. Nat. size.

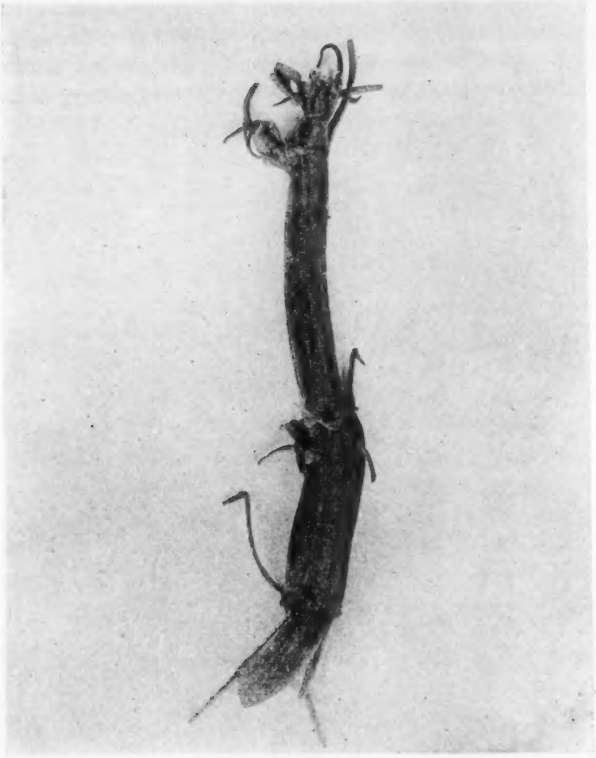

FIGURE 6.—Fasciation in *Fagopyrum tataricum*. A highly fasciated branch displaying a flattened ribbon-shaped condition throughout its entire length. Nat. size.

leaves and branches can be clearly seen, which are numerous and whorl-like crowded around the nodes. Quite often branches were found to be flattened in distinctly ribbon-like fashion throughout their length, in which case they would rarely split but continue in that condition narrowing gradually towards the summit where they would resolve themselves into numerous proliferating shoots, leaves and flowers (figure 6); often fasciated branches of this type were bent, owing, undoubtedly, to unequal growth.

A rather interesting fasciated branch was observed on a fifth-generation plant that grew in pot 64 in the greenhouse at the AROOSTOOK FARM, and had originated from a four-angled fruit of plant 5, from pot 37 of

the fourth generation. A rough diagrammatic sketch of that branch is given in figure 7. This branch originated in the axil of the first leaf above the cotyledons. It was 1.2 mm thick and 4 mm wide for a distance of 21 cm. At this point the branch twisted itself to the right and split in the middle: the two separated parts enclosing a more or less triangular space. This split was probably caused by tissue tension in the knee-shaped bend. The upper separated part of the branch measured 2 mm, the lower 2.5 mm in width. Just above the point where the branch resumed its undivided aspect again, it measured 5.5 mm. From that point the branch turned upwards twisting round its axis from right to left for a distance of about 1.5 cm when it ran almost horizontally twisting again round its axis. The width measured here was 5 mm. At this point the branch turned inward measuring 4 mm in width and terminating, perfectly ribbon-shaped, in a cluster of fruits. The leaves, with the exception of the first one, showed altered phyllotaxy. Four pairs of leaves developed bearing in their axils fruits on short peduncles. At the point where the branch took a nearly horizontal course a pair of rudimentary leaves developed with a cluster of fruits distributed around the node. At the apex of the branch the largest cluster of fruits was produced with no trace of leaves.

With regard to the transmission of the fasciated character our race exhibited a dimorphism characteristic of the ever-sporting varieties. The figures in table 24 illustrate the behavior of the fasciated character in plants of the fifth generation that grew under favorable conditions of nutrition.

TABLE 24

Source of fruits	Number of plants	Number of fasciated plants
Pot 36	25	7
Pot 37	11	4
Pot 38	8	5
Pot 39	27	15
Pot 42	16	10
Pot 44	11	5
Pot 47	8	5
Total	106	51

The fasciation thus was reproduced in half of the progeny. Pending the further behavior of the fasciated character of this strain in subsequent generations and its analysis by crossing, the question of its heredi-

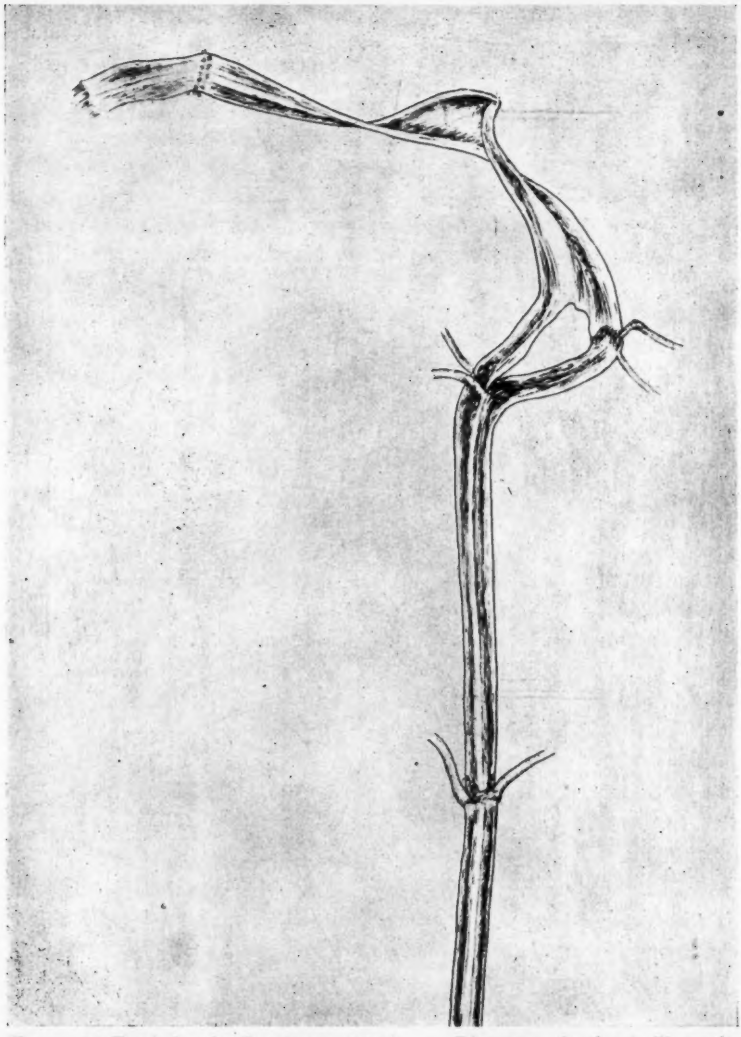

FIGURE 7.—Fasciation in *Fagopyrum tataricum*. Diagrammatic sketch illustrating a peculiar case of fasciation.

tary transmission cannot yet be definitely answered. The manifestation of this character was first noted in plants that grew under crowded

conditions in pots. In the following generation, under favorable conditions of nutrition, this character at once asserted itself in a manner typical of the fasciated races. It is important to state here that the slightly varying line No. 22, though grown under the same conditions of environment as line No. 5, was never found to exhibit fasciation even in a single individual. All external agencies, as traumatic stimuli, insects, etc., had the same chance of operating upon the individuals of both lines in the direction of evoking fasciation, as the progeny of both lines grew side by side, and in some instances, in the same pots. We must note then the fact that, whatever the nature of this fasciation, the two strains react in a different manner to the influence of the same environmental agencies, as evinced by their different phenotypic appearance.

Notwithstanding these considerations it is realized that it is premature to commit oneself on the question of hereditability of this fasciation. It would be equally premature to *a priori* deny the hereditary character of the fasciation in question as some writers do with most of the fasciated races of DE VRIES which they dismiss as mere somatic modifications without previously furnishing the necessary experimental evidence from a genetical analysis of the cases. The fact that certain experimenters succeeded in evoking fasciations through artificial stimuli or operation of parasites does not necessarily disprove the interpretation of most of DE VRIES's fasciations as hereditary characters. It is well known that most of the fasciated races exhibit a "fixed dimorphism," one part of the progeny displaying the character of fasciation and the other part appearing perfectly normal. This latter group, however, is only apparently normal for in the next generation they reproduce, under similar conditions of environment, the same proportion of normal and fasciated plants as the members of the fasciated group, much in the same fashion as the fruits of a short-styled plant of the heterostylous *Fagopyrum esculentum* produce short-styled as well as long-styled plants in about equal numbers. It is clear then that it is incumbent upon those who from instances of artificially evoked fasciations draw conclusions disproving the hereditary character of most of the fasciations, to prove that the material that reacted to external stimuli with the formation of fasciation did not belong to the group of phenotypically normal plants but with a genotypic condition for fasciation originally present.

External agencies may well induce fasciations operating as a *releasing* agency in cases where the factor for fasciation is present, much in the same fashion as temperature causes chemical reactions to take place;

but there seems to be no available evidence showing the external agencies to be the direct *causal* factor in the etiology of fasciations. The fact that artificially induced fasciations have been established in the very plants (*Zea Mays,* Oenothera, *Raphanus raphanistrum, Picris hieracioides*) which without provocation by external injurious agencies, spontaneously develop fine specimens of fasciation, very strongly suggests that the fasciations following upon external injuries are a secondary phenomenon contingent upon a genotypic condition for fasciation already present. In this connection it is of interest to note that PEYRITCH (cited by GOEBEL 1900, part I, p. 188) whose researches into the teratological development as induced by external injurious agencies, are well known, clearly distinguished between "the immediate *determining* cause, which in many cases may be an external agent, and the internal factor, namely the *predisposition* to the development of the anomaly. It is easy to convince oneself that all the individuals of the same species do not react in the same way towards the same external injurious agencies, and that their reaction also varies at different times."

OBSERVATIONS ON THE INFLUENCE OF THE ENVIRONMENT UPON TERATOLOGICAL DEVELOPMENT IN *Fagopyrum tataricum*

In dealing with the behavior of ever-sporting varieties DE VRIES (1910, p. 307) emphasizes with great stress the dependence of their "semi-latent" characters upon the external conditions of life. His observations and experiments led him to the conclusion that "increased nutrition favors the development of the anomaly."

BAUR (1907) formulated a theory based chiefly upon the observations of DE VRIES, and designed to explain the behavior of ever-sporting varieties like *Dipsacus silvestris torsus* or even Matthiola as specific instances of modifications determined by external factors, nutritional factors in the broadest sense.

In view of the great importance attached to nutrition as highly influencing or even directly determining the characters of the ever-sporting races, it seemed desirable to test the influence of nutrition upon the race dealt with in this paper.

In the experiments to be now described the behavior of this race was studied in different nutritional media and in different environments. The media used were composted soil, ordinary soil and sand. As to environment, the cultures were grown under greenhouse conditions and in the garden. Two greenhouses were used whose conditions differed greatly,

notably with respect to humidity and temperature. In the greenhouse of the UNIVERSITY prevailed what might be called a moist and hot condition. The temperature was uniform, varying only slightly from 24° C during the day to 21° C at night. The greenhouse at the AROOSTOOK FARM where the cultures grew in the summer, no artificial heat was used, the temperature following the natural daily amplitude. The air in this greenhouse was dry.

The effect of deficient nutrition or starvation was studied through five generations and in each generation from the second on the plants grown in sand or gravel originated from fruits of plants that also had grown under conditions of starvation. Thus subjecting a part of our cultures to the influence of starvation from generation to generation a pure sand strain has been obtained which offered the opportunity of studying not only the effect of the immediate starvation medium but also the influence of a continued operation of deficient nutrition affecting the plants of each generation in their ontogeny, during the critical period of seed formation, in the course of which, according to the observations of DE VRIES and of EAST and HAYES (1914, pp. 35 and 47) certain plant characters are susceptible to the operation of environmental agencies.

A portion of the fruits of the original plant from which line No. 5 descended was planted in an 8-inch pot No. 2 filled with soil that was mixed with commercial fertilizer. The other portion of the same crop was planted in pot No. 2a filled with soil that was mixed with a considerable amount of sand. Both pots were placed in the UNIVERSITY greenhouse.

The appearance of the sand cultures did not differ very markedly from those in the fertilized soil. The detailed account relating to the variation of the plants in these 2 pots is given in tables 1 and 3, respectively. From the almost identical manifestation of abnormality in both series it may be concluded that the poor medium in pot No. 2a had no limiting effect in the development of abnormal blossoms.

The fruits from pot No. 2 were planted in the summer of 1916, in pots filled with good soil mixed with fertilizer, while the fruits from pot No. 2a were planted in pots containing gravelly sand. The pots of both series were placed side by side in the garden. The ratios between the normal and abnormal flowers in both series are given in table 25.

The plants in the rich soil yielded twice as many fruits as those in the sand but as will be seen from the above figures, the mode of variation in the gynoecium is strikingly similar in both series.

TABLE 25

	Fertilized-soil series				Sand series			
Number of carpels.....	3	4	5	6	3	4	5	6
Actual frequency	864	396	34	1	486	233	10	1
Percentage frequency ...	66.71	30.58	2.63	0.07	66.57	31.92	1.37	0.13

In the following season the plants of each of the two series were subjected to the treatment accorded their respective mother plants. The pots of both series were again placed out-doors. The plants in the rich soil made a tall growth with a relatively moderate amount of branching in the lower parts of the plant body, while the sand cultures were of a low stature. The results from both series are shown in table 26.

TABLE 26

	Rich-soil series				Sand series			
Number of carpels.....	3	4	5	6	3	4	5	6
Actual frequency	1366	1000	112	4	520	559	68	2
Percentage frequency ...	55.04	40.29	4.51	0.16	45.26	48.65	5.95	0.17

The plants in the sand series actually yielded a higher percentage of abnormal flowers than those in the rich soil.

The behavior of the two series under their respective treatment was again studied in the fourth generation grown in the UNIVERSITY greenhouse. The progeny of the plants of the rich-soil series were grown in ordinary and composted soil, in pots 36-39; the progeny of the plants in the sand series were grown in sand, in pots 43 and 44. The morphological features of the plants in 36-39 will be recalled from the discussion given in a previous section. They made a compact growth marked by differentiation and branching in the lower part of the plants (figures 8 and 9).

The plants in pots 43 and 44 that had originated from fruits of "starved" parents presented a rather interesting aspect. They were of very low stature, dwarf-like in appearance, reaching a height of only 6 to 12 centimeters (see figure 10). The leaves of these plants were small and their number slightly lower than in the plants originated from well nourished parents (cf. EAST and HAYES 1914). The size of the corollas and of the fruits was normal.

The examination of the flowers of the plants grown in composted soil,

TABLE 27

Medium	Number of carpels																Synanthies
	3	4	5	6	7	8	9	10	11	12	13	14	16	17	18	19	
Composted soil ..	16.28	67.14	8.64	2.11	0.82	0.74	0.52	1.08	0.14	0.71	0.17	0.06			0.06	0.06	1.49
Ordinary soil	19.50	67.05	7.73	1.33	0.66	0.88	0.57	0.55		0.09			0.04				1.50
Sand	17.36	61.43	13.61	1.95	0.51	0.41	0.10	0.41	0.10	0.10		0.10		0.10			3.81

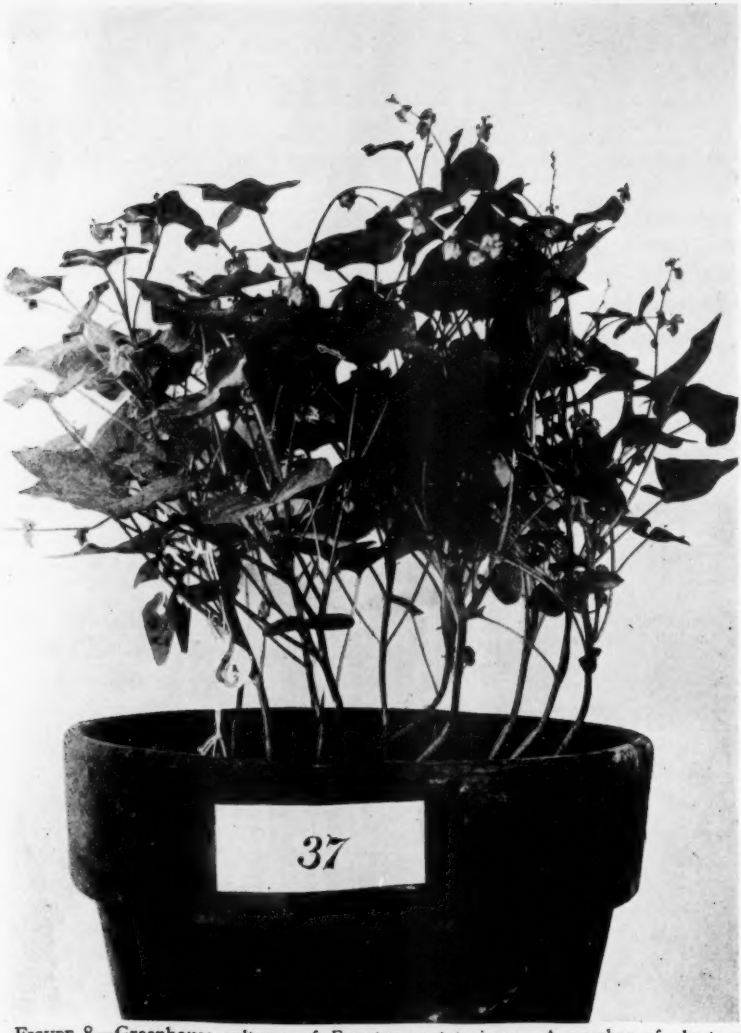

FIGURE 8.—Greenhouse cultures of *Fagopyrum tataricum*. A number of plants of the ever-sporting line No. 5, grown in ordinary garden soil. × .4.

normal soil, and sand, gave the results in table 27, expressed in percent.

These figures bear out the results obtained from the first generation

FIGURE 9.—Greenhouse cultures of *Fagopyrum tataricum*. Plants of line No. 22 grown in composted soil. × .4.

indicating that under the conditions prevailing in this greenhouse rich nutrition or starvation has no visible effect upon the development of ab-

FIGURE 10.—Greenhouse cultures of *Fagopyrum tataricum*. Dwarfed plants of line No. 5 grown in sand. × .4.

normal flowers. Starvation had a marked effect on the habit of the plants affecting such characters as height and number of leaves.

This experiment was again carried out with cultures of the fifth generation. The plants of the sand series were grown in pots and placed in the garden. The plants originated from the well nourished parents were grown in the garden under very favorable conditions of nutrition, each plant occupying 2 feet each way. The sand series yielded 53.13 percent of normal and 46.87 percent of abnormal fruits. The garden plants yielded 50.78 percent of normal and 49.22 percent of abnormal fruits.

From the evidence furnished by the above experiments the conclusion may be drawn that under conditions favoring the maximum degree of abnormal development optimum nutrition or starvation has no visible effect upon the degree of manifestation of floral abnormalities in the race dealt with in this paper. With the elimination of nutrition as a stimulating factor of environment, all the evidence obtained from the behavior of this race under different environments, notably the identical mode of variation of the first and fourth generation grown in hot and moist air, points to high humidity and temperature as the factors

FIGURE 11.—Greenhouse cultures of *Fagopyrum tataricum*. Plants of line No. 5 grown in sand and scantily watered. × .4.

favoring the maximum expression of abnormal development.[2] Instances showing the development of abnormalities to be dependent upon factors of environment other than nutrition, are by no means rare. Thus a mutation in Drosophila, the reduplication in the legs, discovered by Miss HOGE (1915), was found to be dependent upon low temperature for its realization. Another mutation in the same fly, "abnormal abdomen," reported by MORGAN (1915), was shown to be determined by the amount of moisture in the food.

Where the conditions of environment, necessary for the realization

[2] It is conceivable that the reduced volume and intensity of the light in the early spring months as compared with that of the summer months, may have influenced the teratological development in the first and fourth generation of this race. However, neither the habit of the plants, nor the daily recorded mode of variation seemed to support this assumption.

of the maximum of abnormal development are not present in the required degree, as in the cool and dry greenhouse, starvation and other detrimental agencies may assert their influence upon the development of abnormality. Some evidence supporting this point may be gathered from the following experiment. In connection with the growing of the fourth generation of this race, an attempt was made to determine the combined effect of starvation and lack of water under greenhouse conditions. Accordingly, some 26 plants that had originated from well nourished parents were grown in an 8-inch pot filled with sand and placed in the UNIVERSITY greenhouse in which hot and moist air prevailed. The plants were watered only very scantily,—barely enough to keep them from drying up. As a result the plants were stunted (figure 11) with thin stems and hardly any secondary branches. The extent of the stunting in growth can be seen by comparing the measurements of the laminae of both cotyledons of these plants with those of the normal plants grown in rich soil and well watered. Both cotyledons of each plant were measured, 2 diameters of each lamina being taken: the diameter in the plane of the stalk (d_1) and one at a right angle to it (d_2). The measurements were recorded for 10 plants in each series. The average length, with the normal plants, of d_1 was 17.05 mm and of d_2 19.75 mm, while the same dimensions with the plants of the sand series were 10.86 mm and 12.42 mm, respectively. The examination of the flowers of 8 plants grown in sand and scantily watered gave the results tabulated in table 28.

TABLE 28

	Number of carpels						Synanthies
	3	4	5	6	7	8	
Actual frequency	47	223	16	2	1	1	3
Percentage frequency ...	16.03	76.11	5.46	0.68	0.34	0.34	1.03

From these figures it will be noted that the ratio between the normal and abnormal flowers, 16.03 : 83.97, of this series is practically the same as in the well watered cultures grown in composted soil (16.28 : 83.72).

The same experiment was carried out in the cool and dry greenhouse at AROOSTOOK FARM. The results obtained from the normal, well nourished and watered cultures, from normally watered sand-cultures and from scantily watered sand-cultures are given in table 29.

TABLE 29

Medium	Treatment	Percentage ratio between normal and abnormal flowers
Rich soil	Well watered	34.58 : 65.42
Sand	Well watered	46.36 : 53.64
Sand	Scantily watered	68.40 : 31.60

These figures in conjunction with the results obtained from the plants grown in hot and moist air clearly indicate that under conditions void of optimum moisture and temperature necessary for the maximum development of abnormality, the influence of deficient nutrition and lack of water becomes apparent but that the effect of these detrimental factors is nil when they operate in the presence of other factors of environment which control the maximum manifestation of the abnormal character.

SUMMARY

The more important observations recorded in this paper may be summarized as follows.

An ever-sporting race of *Fagopyrum tataricum* has been isolated and its characters studied for 5 generations under varying conditions of environment.

The variations here considered occur in the gynoecium, the perigone, and the vegetative organs of this race.

The variations in the gynoecium are characterized by the production of supernumerary carpels. The number of carpels per pistil was found to vary from 3 up as high as 25. Under ordinary conditions of growth the number of flowers with normal gynoecia is greater than or equal to the number of flowers with abnormal gynoecia. Under conditions favoring the development of abnormal flowers the variation is bilateral, and can be represented by a curve the apex of which is formed by the abnormal four-carpelled flowers.

The frequency of flowers with abnormal gynoecium decreases as the number of aberrant carpels per pistil increases.

Associated with the abnormal gynoecia are abnormal perigones with a varying number of segments ranging from the normal number 5 as high as 18. The favorable conditions capable of transforming the unilateral variation of the gynoecia into a bilateral one, failed to affect the perigone in the same manner. The variation in the number of perigone leaves remained unilateral with the frequency of the normal, five-parted perigone forming the apex of the skew curve.

The frequency of the normal, five-parted perigone decreases as the number of carpels per pistil increases.

Floral prolifications in the form of various types of synanthous flowers, often giving rise to syncarpous fruits, were found to be produced generation after generation in fairly constant proportions under given conditions of environment.

The teratological development of the vegetative organs in the form of more or less developed fasciations was reproduced, under favorable conditions of environment, in 50 percent of the offspring.

All the descendants of the ever-sporting race reproduce the ever-sporting type of the mother plant regardless of whether they originated from normal or abnormal fruits of the parent.

The ratio between the normal and abnormal flowers was found to be a function of the environment. Under a given set of environmental conditions this ratio as well as the relationship between the different forms of the abnormal flowers *inter se* is constant to a very marked degree.

Selection carried on for 5 years had no visible effect upon the type and range of teratological development of this race. The ever-sporting strain after isolation at once displayed the highest degree of abnormality reached in the subsequent generations under similar conditions of environment.

Under conditions controlling the intensity of abnormal development, optimum nutrition or starvation, while affecting the habit of the plants, appeared to have no effect upon the degree of manifestation of abnormalities. The evidence from the study of this race under different conditions of environment points to high humidity and temperature as the factors favoring the expression of abnormality. Under unfavorable conditions of humidity and temperature, the influence of starvation and lack of water upon the degree of abnormal development was noted.

The results of a study of the frequency distribution of the different types of flowers upon the plant point to the existence of a definite region on the plant in which the tendency to vary and proliferate is most pronounced. Considering the plant as a whole, this region is confined to the basal, differentiated parts of the plant. The first three branches on the main stem from below, especially the second one, mark the seat of greatest abnormal development, while the 4th, 5th, and 6th branches show a low degree of variability as well as the lowest absolute number of flowers. In the basal region of the terminal raceme the output of flow-

ers and the range of abnormality again increases. Similar but more marked differences prevail in the individual branches of the second and third order. Here, it is again the buds in the axils of the second leaf and in the basal region of the terminal raceme that show the greatest relative number of abnormal flowers as well as the greatest range of variability as measured by the frequency occurrence of the most aberrant variants.

Relative to the frequency of occurrence of the different types of flowers at different periods of the flowering season, under the prevailing conditions, the first and second week of the flowering season mark the lowest relative production of abnormal flowers, after which a marked increase in the output of abnormalities follows when the secondary and tertiary branches begin to develop their flowers. Toward the end of the flowering season the upper regions of the plants produced only a very few flowers while the lower differentiated parts of the plants sustained their flower production to the end of the flowering season.

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AN HEREDITARY COMPLEX IN THE DOMESTIC FOWL

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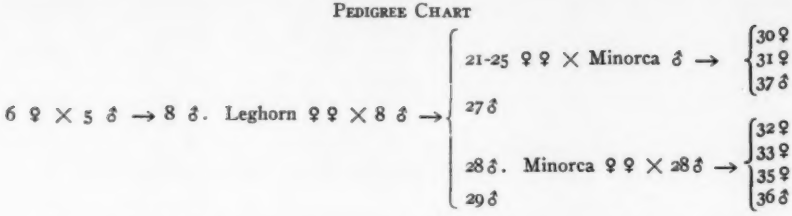
Brachydactyly, syndactyly, and leg-feathering or ptilopody[1] are among the many characteristics of the domestic fowl that have been studied from the standpoint of genetics. The last in particular, owing to its widespread occurrence, has aroused especial interest. Its heredity has been investigated by HURST (1905), DAVENPORT (1909), and more recently by PUNNETT and BAILEY (1918). The genetic behavior of syndactyly has been studied by DAVENPORT (1909) and that of brachydactyly by DANFORTH (1919 a).

The purpose of this paper is to present evidence that these three characteristics, at first sight apparently distinct and unrelated, are in reality the product of a single gene or a single combination of genes. The possibility that this is the case was suggested in the earlier paper on brachydactyly, but at the time that paper was written, sufficiently critical breeding tests had not been made, the suggestion being based largely on morphological evidence. The additional data now available, while not abundant, seem to be significant, and are therefore put on record.

Except where otherwise indicated the descriptions and data are all from individuals derived, on one side at least, from a single family, the relationships of the principal members of which are shown in the accompanying pedigree chart. None of those indicated in the chart was syndactyl.

[1] Two terms, "leg-feathering" and "booting" have been employed to indicate the presence of feathers on the tarsus and toes. Both of these terms are inappropriate; the former because it is not the leg, but the tarsus and toes that is meant, the latter because the term is already in use to indicate a fusion of tarsal scutella. Since no other convenient term seems to be available the word ptilopody (πτίλον, feather; πούς, foot) is used in this paper to designate the condition in which down or feathers tend to appear on the tarsus and toes.

PEDIGREE CHART



The individuals of mixed ancestry may be characterized as follows:

No. 5. Male. A mongrel of unknown ancestry, but with a general appearance suggestive of Brahma extraction. Moderately ptilopod. No record as to bracydactyly.

No. 6. Female with three legs (Pygopagus parasiticus). Small, showing no indication of Asiatic origin. Neither brachydactyl nor ptilopod.

No. 8. Male. Brachydactyl, ptilopod.

Nos. 21-25. Females. Brachydactyl, ptilopod.

No. 27. Male. Brachydactyl, ptilopod.

No. 28. Male. Brachydactyl, ptilopod.

No. 29. Male. Not brachydactyl, ptilopod.

No. 30. Female. Not brachydactyl, not ptilopod.

No. 31. Female. Brachydactyl, not ptilopod.

No. 32. Female. Brachydactyl, not ptilopod.

No. 33. Female. Brachydactyl, not ptilopod.

No. 35. Female. Not brachydactyl, ptilopod.

No. 36. Male. Brachydactyl, not ptilopod.

No. 37. Male. Brachydactyl, not ptilopod.

Chicks were raised from these birds, bred together and with barred Plymouth Rocks, White Leghorns or Black Minorcas. The distribution of brachydactyly, ptilopody and syndactyly among the offspring is indicated in table 1 where chicks and embryos of 13 days and over are considered. (Besides those shown in the table, 305 additional chicks were produced by some of these parents after having been treated with alcohol. Of these 49 percent were brachydactyl, 37 percent ptilopod and 0 percent syndactyl. 50 percent of them showed either brachydactyly or ptilopody. These data are not included here. The effect of alcohol on the distribution of traits is discussed in another paper (DANFORTH 1919 b).

The table shows first of all a high degree of correlation between brachydactyly and ptilopody. The correlation, however, is not complete

TABLE 1

Parental matings and offspring.

Parental traits and matings	Distribution of traits in the offspring (Data from 508 chicks of thirteen days and over)			
	Brachydactyl ptilopod	Brachydactyl non-ptilopod	Ptilopod non-brachydactyl	Non-ptilopod non-brachydactyl
I. Brachydactyl ptilopod × normal				
1. Leghorn ♀♀ × 8 ♂	49	2	5	78
2. Barred Plymouth Rock ♀♀ × 8 ♂	2	0	0	1
3. Minorca ♀♀ × 27 ♂	15	7	0	45
4. Minorca ♀♀ × 28 ♂	49	10	3	66
5. 21-25 ♀♀ × Minorca ♂	23	21	0	65
Total	138	40	8	255
II. Non-brachydactyl ptilopod × normal				
6. Minorca ♀♀ × 29 ♂	7	5	1	11 (19)
7. 35 ♀ × Minorca ♂	3	5[1]	0	2
Total	10	10	1	13 (21)
III. Non-ptilopod brachydactyl × normal				
8. Minorca ♀♀ × 37 ♂	4	5	1	7
IV. Non-ptilopod brachydactyl × non-ptilopod brachydactyl				
9. 32 ♀ × 37 ♂	2	2	0	1
V. Bracydactyl ptilopod × brachydactyl ptilopod				
10. 21 ♀ × 28 ♂	6[2]	0	0	4
VI. Miscellaneous				
11. 21-25 ♀♀ × 27-28 ♂♂	9	1	1	8
12, 21, 30, 33, ♀♀ × 36 ♂	6[1]	3	0	3
Total	15	4	1	11
Number in each class, irrespective of ancestry	175	61	11	291 (299)

[1] One of these was syndactyl.

[2] Two of these were syndactyl.

since some individuals are brachydactyl but not ptilopod while others are ptilopod without being brachydactyl. This immediately suggests linkage of genes and "crossing over." At the time the first paper was written this possibility could not be excluded, although it was pointed out that the fact that the two traits tend to parallel each other in their fluctuation does not favor such an interpretation.

The results of matings 6-9 seem to settle the question of two possible linked genes. In mating 6 the male was not brachydactyl but did have a very few small feathers on the tarsus and fourth toe. Mated to normal Minorca hens which did not carry determiners for either brachydactyly or ptilopody he produced both brachydactyl and ptilopod offspring. Mating No. 7 represents the reciprocal cross and yielded similar results except that, probably owing to the small numbers, no long-toed ptilopod chicks appeared. Mating 8 between a brachydactyl male with no feathers on the tarsi or toes and normal Black Minorca hens likewise yielded chicks that showed brachydactyly only, ptilopody only, brachydactyly and ptilopody combined, and the absence of both traits. Finally mating 9 in which neither parent showed ptilopody gave two chicks that were both brachydactyl and ptilopod, two that were brachydactyl only, and one that was neither.

These results seem to exclude the possibility of the different somatic combinations being due to separation of linked genes. If there are indeed two genes there is no evidence that they are ever separated since individuals showing one trait and lacking the other reproduce the missing trait as readily as those that actually have it. So far as breeding tests show, brachydactyly and ptilopody may be regarded as two manifestations of the same hereditary factor.

This interchangeability of brachydactyly and ptilopody may possibly explain some supposedly aberrant cases discussed by PUNNETT and BAILY (1918). In one case (*loc. cit.*, p. 208) a female derived from a Langshan-Hamburg cross had no feathers on the tarsi or toes but nevertheless behaved in breeding tests like a true ptilopod individual. It will be apparent that if this particular bird were brachydactyl, its behavior was entirely in accord with expectations and could not be regarded as in any way aberrant.

Similarly on p. 212, in discussing some work of BONHOTE (1914), PUNNETT and BAILEY quote a case in which two clean-legged F_1 birds from a Silky-Yokohama cross when bred together gave 8 ptilopod and 16 clean-legged offspring. If, as is highly probable, the F_1 parents were brachydactyl, the mating would be entirely comparable to mating 9 in

the table and the results are essentially the same since in both cases ptilopod and non-ptilopod young were produced. The total number of chicks in this case is so small that the relative size of the two classes has little significance especially when it is recalled that some of the 16 chicks recorded as clean-legged may nevertheless have been brachydactyl.

Likewise the data on which DAVENPORT (1909) based his statement that "two extracted clean-footed birds sometimes throw boot and sometimes not" may have come from matings in which at least one of the individuals involved was brachydactyl. In other words, if the interpretation suggested here be accepted, one of the difficulties encountered by students of ptilopody will have been removed.

The failure to recognize brachydactyly as another form of ptilopody tends in some measure to vitiate the observations thus far reported. For example, in the results from matings recorded in this paper it would make a difference of over 10 percent whether the brachydactyl non-ptilopod group were counted on one side or the other. This is a matter of considerable importance in an investigation of the genetic behavior of a trait.

The evidence for associating syndactyly with the other two traits is less conclusive but is such as to create a very strong presumption in favor of the view that such an association exists. DAVENPORT (1909) has described the trait in detail and indicated its range of variability. His data come from about one hundred and fifty individuals all descended from a single Brahma hen which was herself somewhat syndactyl. It is clear from the descriptions and figure that the progenitor of this family was also ptilopod. It is apparent too that many, possibly all, of her syndactyl descendants were likewise ptilopod. DAVENPORT'S data show clearly that the trait is dominant.

Only four syndactyl chicks were obtained from the experiments reported in this paper. Two came from mating 10 and one each from matings 7 and 12. None of the parents of these four chicks was in the least syndactyl nor did syndactyly occur elsewhere in the immediate ancestry. The chicks themselves were all brachydactyl; those from matings 10 and 12 were also ptilopod. The appearance of a normally dominant trait in this manner adds some support to the suggestion that the condition found in the parent is really the same trait in a different form. Unfortunately none of these syndactyl chicks became available for breeding tests.

Another thing that strongly suggests the common origin of the three traits is the fact referred to in the paper on brachydactyly, that the same

combination of traits tends to occur in the pigeon. It is much simpler to suppose that a single mutation has occurred in one homologous gene of the pigeon and fowl than that three different genes have undergone mutation at the same time and in the same manner in these two very different species.

On the basis of the data that have now been presented the simplest and most adequate working hypothesis would seem to be that the three morphologically distinct traits, brachydactyly, syndactyly and ptilopody, owe their existence to the action of a single gene. The tendency of the trait to manifest itself in some crosses more frequently in one form, and in other crosses in another, is perhaps to be explained by the action of modifying genes unequally distributed among individuals and is in harmony with DAVENPORT's observation that within a single manifestation (ptilopody) the grade represented by the parent shows some tendency to be reproduced in the offspring.

The characteristics and to some extent the ontogeny of these traits have been discussed by the authors to whose work reference has already been made.[1] One point, however, seems to have been entirely overlooked in previous studies of the subject, namely, the range within which the ptilopod trait varies. Ptilopody involves not only the usual presence of feathers on the tarsus but also rather fundamental changes in the scales of the foot. A normal non-ptilopod individual shows scutella arranged with great regularity over the lateral side of the tarsus and along the dorsum of the fourth toe. In the Minorca, for example, (figure 1) there are about 31 such scales in linear sequence, 17 on the toe and 14 on the tarsus. These numbers are subject to some variation but are reasonably constant. The scales themselves are smooth and regular with the distal free margins approximately straight and parallel. Only rarely is a scale divided. In ptilopod specimens (figures 2 and 3) not only are some of the scales reduced in size and thrown out of alignment but they are modified structurally, frequently showing a tendency to become raised and cylindrical. In some instances forms occur which are intermediate in character between scales and feathers. Where the reduction is carried still farther the tarsus and toe may be essentially smooth but with some of the individual scales showing longitudinal lines and grooves (figures 4 and 5). This sculptured appearance is almost always

[1] "Le vieux coq," a well known etching by the artist Felix Bracquemond, which is doubtless to be found in most museums of fine arts, portrays with remarkable fidelity all the peculiarities mentioned here except syndactyly.

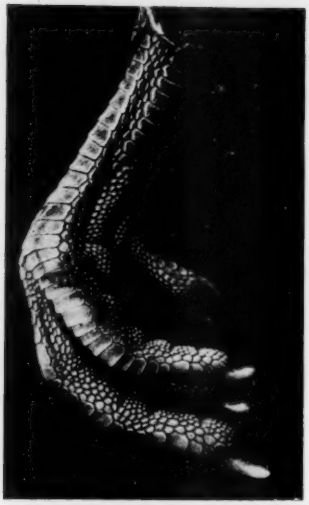


FIGURE 1.—Lateral aspect of the left foot of a Black Minorca chick showing normal proportions and the usual arrangement of scales on the antero-lateral aspect of the tarsus and on the dorsum of the fourth toe.

associated with some irregular imbrication of the scales. A series of individuals could easily be arranged to show a complete gradual transition from a condition with only a few irregular and sculptured scales to one with the heaviest degree of feathering. Indeed it might perhaps be more accurate to regard the ptilopod factor as one primarily affecting the scale-forming tissues of certain parts of the foot. In its mildest manifestation only the scales are involved. In slightly more pronounced instances there appears in addition a modified quill or rudimentary feather, generally on the basal phalanx of the fourth toe. Further intensities of manifestation may be traced through the ten stages recognized by DAVENPORT. Morphologically each feather may represent a part of the rudiment which, in the absence of the ptilopod factor, would have gone into the formation of a scale.

Despite the fact that the three traits are morphologically very different —webbing of the toes, modification of scales or feathers, and reduction in the size and number of bones are quite unlike—the possibility of their being traceable to the action of a common gene is by no means excluded. It is now commonly admitted that each gene in the germ plasm tends to affect all parts of the body more or less but that the reactions in different

FIGURE 2

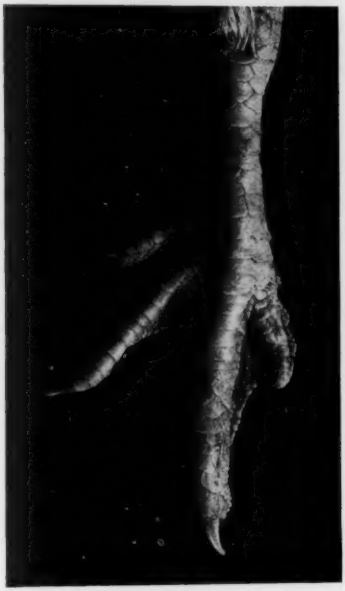


FIGURE 3

FIGURE 2.—Anterior view of a (left) brachydactyl, ptilopod foot. Few of the birds referred to in the body of the paper showed a greater degree of ptilopody than this one. In addition to those on the tarsus and fourth toe a few small feathers may be seen also on the third toe. The brachydactyly which is of the more pronounced type is, as usual, most manifest in the fourth toe. This digit has only two phalanges in place of the normal five. The specimen is not syndactyl.

FIGURE 3.—Anterior view of the left foot of an individual in which the trait is present in all three forms. One or two feathers are present (ptilopody), the fourth toe is greatly reduced (brachydactyly) and the third and fourth toes are fully webbed (syndactyly).

parts may be quite diverse. With the cases in question it is easy to imagine that a disturbing factor coming into action on the 7th-8th days of incubation might be effective in producing permanent webbing of the toes. This is the time when the webbing, already present in the normal embryo, shows its most rapid involution and might be expected to be most susceptible to modifying influences. The same factor becoming effective on the 8th-10th days might be too late to have any effect on the webbing of the toes but would find the cartilages in their formative, and

FIGURE 4

FIGURE 5

FIGURE 4.—Lateral view of a left foot showing no feathering whatever but clearly revealing the presence of the ptilopod factor by the irregularities in the scutella, some of which are "sculptured" (A). The specimen is moderately brachydactyl, the dorsal scutella being reduced from the normal 17 to about 10. The third and fourth toes are fully webbed. The falciform free margin of the web is indicated at B.

FIGURE 5.—Right foot. Similar to figure 4, but showing the sculpturing of the scales more clearly. There is a slight indication of syndactyly. Figures 4 and 5 should be compared with figure 1 in reference to the number, form and arrangement of scutella and the relative lengths of the toes.

therefore, perhaps, most susceptible stage. Finally, if not effective before the 11th-12th days, the normal webbing and skeleton of the toes would have already been determined but the possibility of feather-germ development would still remain. (For a discussion of the embryological relations of these traits the reader is referred to the paper on brachydactyly (DANFORTH 1919 a).

If one may be permitted to speculate on the mode of production of such traits several possibilities at once suggest themselves. (a) The simplest and crudest explanation suggests that the observed manifestations are the product of the action of some internal secretion upon the

normal tissues of the foot. In this case we are in reality studying the hereditary character and fluctuations in an endocrine gland through the effects produced by its secretion. (b) Conversely it might be assumed that the effect of the factor is to "sensitize" certain parts to some normal product of the endocrine system. (c) Still again, it is possible that the factor acts intrinsically and when a certain stage of development is reached the presence of a given gene in each cell of a rudiment determines the behavior of the whole mass, more or less irrespective of developments in other parts of the embryo. The problem of deciding among these and other possible alternatives belongs in the field of experimental embryology, but is necessarily of interest also to genetics.

Two interesting points raised by PUNNETT and BAILEY (1918) call for brief consideration in this connection. One of these concerns their suggestion that in the Cochin and Dark Brahma races "two factors *A* and *B* may be present, either of which determines leg-feathering," while in the Langshan and Silky only one such factor is present. The data here recorded throw no direct light on the question since no evidence appears to indicate the presence of more than one factor. But since the progenitor of these birds was a hybrid, and since the degree of ptilopody in none of his descendants was very pronounced, it is quite possible that even though the race may have been of Brahma extraction one factor had already been lost from the line of descent when the present breeding tests were begun. PUNNETT and BAILEY seem to imply that factor *A* is the more constant one, and since they offer no means of differentiating between them we may assume that their factor *A* and the gene postulated to explain the brachydactyl-syndactyl-ptilopod complex are the same. If the factor *B* is ultimately isolated in a strain of fowl it will be of considerable importance to determine whether or not it too carries the potentiality of brachydactyly and syndactyly.

The other point brought out in PUNNETT and BAILEY's report is the possible presence of an inhibitor *I*, assumed to be present in certain normal strains and tending to prevent the development of feathers, even in the presence of factor *A*. While, as previously suggested, the particular case for which the *I* factor was postulated is perhaps open to a different explanation, the possibility of such a factor being present in some cases is of interest. Such a factor introduced by the homozygous parent and coming into effect on the tenth to twelfth days might explain the very high percentage of brachydactyl non-ptilopod chicks from matings 5-9. If the existence of the *I* factor can be substantiated, a

more detailed study of its interaction with the peculiar *A* factor may yield interesting results.

To summarize briefly: The data presented in this paper show that ptilopody (the tendency to produce feathers on the tarsi and toes) is subject to a much wider range of variation than has hitherto been supposed, and that the three traits, ptilopody, syndactyly and brachydactyly, are associated in heredity. All the available evidence points strongly to the conclusion that the three traits just mentioned are primarily caused by a single gene. If the conclusions arrived at in this paper are accepted it will be necessary to revise in some measure much of the work that has been done on the heredity of ptilopody ("booting" or "leg-feathering").

The stock used for these experiments was kept in the animal quarters of the Department of Anatomy, the eggs were hatched in the laboratory incubators and the chicks raised for the most part on the roof. The writer wishes to take this opportunity of acknowledging his indebtedness to Dr. R. J. TERRY, Director of the Laboratories, for making these facilities available and for his assistance in many other ways.

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TRICOLOR INHERITANCE. IV. THE TRIPLE ALLELOMORPHIC SERIES IN GUINEA-PIGS[1]

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[Received July 24, 1919]

In a previous paper (IBSEN 1916) mention was made of a fact, at that time fairly well established by the author, that complete extension (E) of black or chocolate pigment, partial extension (e^p) of the same pigments, and non-extension (e) of these pigments, form an allelomorphic series in guinea-pigs. No evidence for this was given at that time because the complete data were to be reserved for a later paper.

Several authors, among others notably LITTLE (1913), had given a different view as to the inheritance of these characters, and it therefore seemed advisable to obtain very complete evidence before presenting it for publication. This has now been obtained, and will be given as briefly as possible in the following pages. Since LITTLE's theory has already been discussed fully in the paper previously mentioned, it will not be taken up again here.

Before proceeding it may be well to mention that the experimental results entirely corroborate the multiple allelomorphic conception. This would of itself exclude every other conception except that of complete linkage, and while these two differ from each other theoretically, they are exactly alike so far as practical results are concerned. In no single instance has a genotype been obtained which was not expected according to theory. The same, however, cannot be said with respect to phenotypes. A few animals have been born which closely resembled an unexpected phenotype, but which when tested proved to be of the expected genotype. This will be taken up later in the discussion.

The one disturbing factor is that the *proportionate numbers of individuals* in a phenotype have not always been according to expectation. This disproportion of individuals in the phenotypes, which does not in

[1] Papers from the Department of Genetics, Agricultural Experiment Station, UNIVERSITY OF WISCONSIN, No. 20. Published with the approval of the Director of the Station.

any way invalidate the allelomorphic relations of the three factors, will also be discussed more fully later.

All of the data have been placed in one large table (table 1). In a triple allelomorphic series 21 different types of mating are possible. These have all been indicated in the table, although in two cases (matings 1 and 2) no matings were actually made.

The offspring have been classified in two ways, (1) the number under each phenotype is given, and (2) those which have been tested are classified according to their genotype. Almost invariably this testing has been done by mating the animal to be tested to a self red (*ee*), this being the lowest in the allelomorphic series.

In each case after the recorded number of offspring a figure is placed in parentheses to indicate the expected number. The method employed in the working out of the theoretical expectation, especially in the case of the genotypes, should be explained. Mating 10 may serve as an example. Of the 87 self black offspring, 14 were tested by being mated to self reds. Of these, 12 proved to be Ee^p, while 2 were *Ee*. According to expectation there should have been equal numbers of each genotype, or 7 and 7. In a similar manner, of the 11 tortoises tested, 3 were homozygous (e^pe^p) and 8 heterozygous (e^pe). Since equality was expected, the number here should theoretically have been 5 of each.

We are now in a position to discuss the matings in table 1. Through mating 6 there is only one kind of phenotype, and the genotypes are close to expectation. In mating 7 we find the first example of genotypic as well as phenotypic disproportion. Instead of 3 blacks to 1 tortoise, the proportion is almost exactly 4:1 (129 self blacks: 32 tortoises, and of the tested self blacks the ratio of Ee^p: *EE* is again almost exactly 4:1, instead of the expected 2:1 (21 Ee^p: 5 *EE*).

A further inspection of the matings shows other disproportions. In mating 8 we have an excess of tortoises instead of self blacks as in mating 7; in mating 9, a deficiency of tortoises, and in mating 13, a surplus of tortoises again. In the other matings the obtained results are fairly, and sometimes quite, close to expectation.[2]

What is the cause of these discrepancies? As yet none has been

[2]It is worthy of mention that in a previous paper (IBSEN 1916) attention was called to the fact that in $e^pe \times e^pe$ and $e^pe \times ee$ matings an excess of self reds occurred in the offspring. In the present paper, with much larger numbers of offspring in these matings, this excess has been cut down till the actual numbers are quite close to expectation. It may possibly be that with larger numbers the discrepancies in some of the crosses reported in this paper may rectify themselves.

TABLE 1

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	c^p Tortoise	*ee* Self red	*EE*	Ee^p	*Ee*	c^pc^p	c^pe	*ee*
1	$EE \times EE$									
	Ee^p♀ × *EE*♂ *EE*♀ × Ec^p♂									
2	Total									
	Ee♀ × *EE*♂	6								
	EE♀ × *Ee*♂	49			0 (1.5)		3 (1.5)			
3	Total	55			0 (1.5)		3 (1.5)			
	c^pc^p♀ × *EE*♂	19				5 (5)				
	EE♀ × c^pc^p♂	0								
4	Total	19				5 (5)				
	c^pe♀ × *EE*♂	30				6 (7)	8 (7)			
	EE♀ × c^pe♂	6								
5	Total	36				6 (7)	8 (7)			

TABLE 1 (continued)

All the possible crosses in the allelomorphic series.

Mating		Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	*ee* Self red	*EE*	Ee^p	*Ee*	e^pe^p	e^pe	*ee*
	ee ♀ × EE ♂	43					8 (8)			
	EE ♀ × ee ♂	71					2 (2)			
6	Total	114					10 (10)			
7	$Ee^p \times Ee^p$	129 (120.75)	32 (40.25)		5 (8.67)	21 (17.33)		1 (1)		
	Ee ♀ × Ee^p ♂	129 (140.25)	58 (46.75)		2 (3.3)	2 (3.3)	6 (3.3)		3 (3)	
	Ee^p ♀ × Ee ♂	37 (38.25)	14 (12.75)		0 (0.7)	1 (0.7)	1 (0.7)		3 (3)	
8	Total	166 (178.5)	72 (59.5)		2 (4)	3 (4)	7 (4)		6 (6)	
	e^pe^p ♀ × Ee^p ♂	18 (12)	6 (12)			1 (1)				
	Ee^p ♀ × e^pe^p ♂	51 (41.5)	32 (41.5)			7 (7)				
9	Total	69 (53.5)	38 (53.5)			8(8)				
	e^pe ♀ × Ee^p ♂	87 (86)	85 (86)			12 (7)	2 (7)	3 (5.5)	8 (5.5)	
	Ee^p ♀ × e^pe ♂									
10	Total	87 (86)	85 (86)			12 (7)	2 (7)	3 (5.5)	8 (5.5)	

TABLE 1 (continued)

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	*ee* Self red	*EE*	Ee^p	*Ee*	e^pe^p	e^pe	*ee*
	ee ♀ × Ee^p ♂	55 (50.5)	46 (50.5)				5 (5)		4 (4)	
	ee ♀ × Ee^p ♂	97 (106.5)	116 (106.5)				7 (7)		3 (3)	
11	Total	152 (157)	162 (157)				12 (12)		7 (7)	
12	*Ee* × *Ee*	74 (73.5)		24 (24.5)	3 (4.33)		10 (8.67)			
	e^pe^p ♀ × *Ee* ♂	17 (23.5)	30 (23.5)			3 (3)			2 (2)	
	Ee ♀ × e^pe^p ♂	35 (53)	71 (53)			2 (2)			9 (9)	
13	Total	52 (76.5)	101 (76.5)			5 (5)			11 (11)	
	e^pe ♀ × *Ee* ♂	83 (85)	41 (42.5)	46 (42.5)		7 (7)	7 (7)		3 (3)	
	Ee ♀ × e^pe ♂	17 (17.5)	11 (8.75)	7 (8.75)		3 (3.5)	4 (3.5)		4 (4)	
14	Total	100 (102.5)	52 (51.25)	53 (51.25)		10 (10.5)	11 (10.5)		7 (7)	
	ee ♀ × *Ee* ♂	71 (70.5)		70 (70.5)			5 (5)			
	Ee ♀ × *ee* ♂	111 (111.5)		112 (111.5)			11 (11)			
15	Total	182 (182)		182 (182)			16 (16)			
16	e^pe^p × e^pe^p		36					1		

TABLE 1 (continued)

All the possible crosses in the allelomorphic series.

	Mating	Offspring (phenotypes)			Tested offspring (genotypes)					
		E Self black (or chocolate)	e^p Tortoise	*ee* Self red	*EE*	*Ee*^{p}	*Ee*	c^pe^p	e^pe	*ee*
	e^pe ♀ × c^pe^p ♂		30 (30)					0 (0.5)	1 (0.5)	
	e^pe^p ♀ × e^pe ♂		21 (21)					1 (1.5)	2 (1.5)	
17	Total		51 (51)					1 (2)	3 (2)	
	e^pe^p or e^pe ♀ × c^pe^p ♂	"3"	112 (115)							
	e^pe^p ♀ × e^pe^p or e^pe ♂		7 (7)					1		
17a	Total		122 (122)					1		
	ee ♀ × c^pe^p ♂		128 (128)						6 (6)	
	e^pe^p ♀ × *ee* ♂		127 (127)						12 (12)	
18	Total		255 (255)						18 (18)	
19	e^pe × e^pe	"5"	133 (138)	46 (46)				6 (4.33)	7 (8.67)	
	ee ♀ × e^pe ♂		84 (85)	86 (85)					6 (6)	
	e^pe ♀ × *ee* ♂		181 (179.5)	178 (179.5)					7 (7)	
20	Total		265 (264.5)	264 (264.5)					13 (13)	
21	*ee* × *ee*		"1"	887 (888)						
	Total	1246	1405	1456						

found, but a certain relation has been noticed. This relation may be stated as follows: In those matings in which both parents are self blacks or else one parent is a self black and the other a tortoise, and in which both self blacks and tortoises occur in the offspring, there is a deficiency of tortoises among the offspring when these are all homozygous (matings 7 and 9) and a surplus when they are all heterozygous (matings 8 and 13). When both classes of tortoises occur in the offspring the excess of one class (the heterozygous) tends to be offset by the deficiency of the other (the homozygous), and as a result the total number is close to expectation (mating 10).

COLE (1914, p. 350) has suggested four possible explanations for modifications of monohybrid ratios. "They might be attributed (1) to the non-viability of a particular class of the F_2 zygotes (as is the explanation offered for both the yellow mice and Antirrhinum); (2) to selective fertilization, i.e., to a selective union of the gametes; (3) to a disproportionate production of the two kinds of gametes; or (4) to a differential viability of the zygotes, but without the complete disappearance of any one class."

No one of these explanations can be made to fit all the aberrant cases just described. The first one, of course, does not apply at all because in none of the matings is one expected class entirely missing. The second explanation, selective fertilization, looks as if it might fit some of the matings, as for instance mating 7. Here one might say that the c^p-bearing gametes tended to unite with those carrying E. The fact that 21 of the 26 tested black offspring were Ec^p would tend to bear this out. On the other hand, if we turn to mating 9, where one of the parents is homozygous for partial extension (c^p), there is still an aberrant ratio in spite of the fact that there is no opportunity here for selective fertilization.

The third explanation, a disproportionate production of the two kinds of gametes, does not apply either, because heterozygous animals of whatever gametic composition when mated to recessive reds (ee) always produce equal numbers of the two expected classes of offspring (matings 11, 15 and 20).

The fourth explanation, the partial viability of some one class, seems to have more in its favor than either of the other three. By referring to table 2 it will be seen that in matings 7 and 9 (in which occur the homozygous tortoises) the average size of litter is comparatively high, while in matings 8 and 13 (which have the heterozygous tortoises) the aver-

GENETICS 4: 602 N 1919

TABLE 2
Average litter size for various matings.

Matings		Total number of offspring	Number of litters	Average litter size
No. 7	$Ee^p \times Ee^p$	161	52	3.10
No. 9	$Ee^p \times e^pe^p$	107	37	2.89
No. 8	$Ee^p \times Ee$	238	91	2.62
No. 13	$Ee \times e^pe^p$	153	56	2.73
No. 10	$Ee^p \times e^pe$	172	62	2.77
No. 11	$Ee^p \times ee$	314	110	2.85
No. 12	$Ee \times Ee$	98	39	2.51
No. 14	$Ee \times e^pe$	205	77	2.66
No. 15	$Ee \times ee$	364	143	2.55
No. 20	$e^pe \times ee$	529	196	2.70
Total		2341	863	2.71

age size of litter is comparatively low. From this one might infer that in the case of the last two matings there is an incomplete viability of the self blacks to account for the excess of tortoises in this mating. But even if this were the true explanation it does not account in the first two matings for the excess of self blacks and consequently the deficiency of tortoises.

When the sex ratios are examined certain aberrancies are found here also. In table 3, which has the matings arranged in the same order as in table 2, it will be found that for matings 7 and 9 the sex ratios are quite close to normal expectation,[3] while in matings 8 and 13 there are marked disproportions. Disproportions occur also in some of the other matings, particularly matings 10 and 14. Why these disproportions should occur it is hard to see since the factors in this allelomorphic series are not sex-linked. Further carefully controlled experimental work is necessary in order to help clear up some of this apparent confusion.

As previously stated, some animals were born that were phenotypically contrary to expectation. This is true of matings 17 a, 19 and 21. The numbers enclosed in quotation marks in table 1 refer to these animals. In the first two of the above-mentioned matings some apparently self-black animals were born from tortoise parents. It had been noticed in a number of cases that animals which were apparently self black at birth later showed a few red hairs and so were undoubtedly tortoises and

[3] The ratio for the total 2341 animals in the table is 105.93 males to 100 females. This approximates that found in many other animals.

TABLE 3
Sex ratios for various matings.

Matings	Sexes of offspring						Unclassified offspring			Total offspring
	E		*e*^{p}		*ee*					
	♂	♀	♂	♀	♂	♀	*E*	*e*^{p}	*ee*	
No. 7 *Ee*^{p} × *Ee*^{p}	67	62	19	13						161
No. 9 *Ee*^{p} × *e*^{p}*e*^{p}	36	33	18	20						107
No. 8 *Ee*^{p} × *Ee*	91	74	29	43			1			238
No. 13 *Ee* × *e*^{p}*e*^{p}	38	14	49	49				3		153
No. 10 *Ee*^{p} × *e*^{p}*e*	42	45	34	50				1		172
No. 11 *Ee*^{p} × *ee*	77	73	77	82			2	3		314
No. 12 *Ee* × *Ee*	38	34			11	11	2		2	98
No. 14 *Ee* × *e*^{p}*e*	41	54	25	25	31	20	5	2	2	205
No. 15 *Ee* × *ee*	93	81			94	79	8		9	364
No. 20 *e*^{p}*e* × *ee*			137	120	131	130		8	3	529
Total	523	470	388	402	267	240	18	17	16	2341

were classified as such. Some of the animals listed as self blacks were born dead and hence had to stay classified as such. The few, however, that remained self black in appearance when adult, behaved as tortoises when mated to self reds (*ee*) or tortoises. It is probable that few if any "selfs" or almost selfs would have been produced were it not for the fact that selection was being practiced in a plus direction in a definite attempt to produce actual *E* selfs in this manner. So far, as above indicated, the attempt has been entirely unsuccessful.

In mating 21 we have another example of an apparent dominant being produced from two recessives. Here, what looked like a tortoise was born from self red parents. The animal in question, A 85.1, was entirely red except for a very small chocolate patch back of the left ear. It was one of a litter of five all of which unfortunately died shortly after birth. The parents have had 14 offspring altogether, and of these 13 were self reds.

The aberrant "tortoise" might be looked upon as a mutation, but evidence based on another animal indicates that it was genetically a self red (*ee*) in which the non-extension factor (*ee*) was "accidentally" over-expressed. The other animal referred to is 665.2, which was red with a few small white patches on the head and a very small black area in front of the right ear. She came from an *e*^{p}*e* × *ee* mating and was originally classified as a tortoise (*e*^{p}*e*) (IBSEN 1916, p. 302). However, when

mated to self reds she had 15 offspring, all self reds. Tortoises as a rule have at least half of the body surface covered with black patches. The two animals, A 85.1 and 665.2, referred to above, had far less black (or chocolate) pigmentation than any genotypic tortoise so far born in our laboratory, and therefore in spite of the black patches on their bodies must be looked upon as genetically self reds.

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INDEX

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Aberrant cases 589, 603–605
Aberrant ratio 603
Abnormalities
  Arcella 111
  Fagopyrum **538, 568, 574**
  Nicotiana 324
  Trifolium 559
  Veronica 559
Accessory factors 6
Accumulation of small heritable variations 148
ACKERT, J. E. 147, *150*
Acquired size, non-heritable 181
ALDERMAN, W. H. 419, *481*
Aleurodes vaporariorum 251, 252, 253
Aleurone 262, 267–**270**, 274, 392
Algae 97
ALLARD, H. A. *340*
Allelomorphs 7, 186, 191, 216, 269, 276–278, 280, 282, 391, 392, 508, 512, 515, 522, 526, 529, 530
Allelomorphic series 278, **597**–600, 604
  Guinea-pigs **597**
ALLEN, C. E. 417, 426, *481*
ALTENBURG, EDGAR 235, 236, 237, *247*
Alternated type of back-cross 296
Amphimixis 96
Amygdalus Davidiana 422
Amygdalus nana × *Prunus persica* 441
Antagonistic heterozygosis 53
Anther 419, 422, 423, 425, 527, 429, 435, 437, 438, 440, 463, 477, 538
Anthocyanin 262
Anthothrips verbasci 252
Antirrhinum 475, 535
Apple (*Pyrus malus*) 459, 469, 471, 472, 481, 485, 487
Apricot (*Prunus armenica*) 420
Arcella dentata **95**–150
  Abnormal specimens 111
  Empty shells **139**–142, 149
  Heredity variation and appearance of diversities during reproduction **95**–150
  Large variations **127**
Arcella discoides 97
Arcella vulgaris 97
Arrangement of genes in the chromosomes 347
Asexual reproduction (see also clones) 142, 181
  Arcella dentata 95–150
  Lemna minor 151–182
Associated factors (see linkage) 270
Association of characters in crosses 263, **270**
Assortative mating 497
Autocatalytic reaction 348
Autosome 526, 530
Auximone 180, 181
BACKHOUSE, W. 418, 452, 454, 476, *481*
BAILEY, E. M. 370
BAILEY, L. H. 446, *481*
BAILEY, P. G. 3, 93, 235, *247*, 587, 589, 595, *596*
Balanced lethal factors 376, 393
BAKER, A. C. 253
BALTZER, F. 234, *247*
BARTLETT, J. M. 370, *393*
BATESON, W. 191, 209, *247*, 354, *355*, 415, 554, *585*
BAUR, E. *247*, 475, *483*, 574, *585*
BEACH, S. A. 419, 467, *483*
Bean (Phaseolus) 311, 340
BEINHART, E. G. 309, *340*
BELLING, JOHN *355*, 464, *483*
BENTHAM, GEORGE 539, *585*
Bimodal distribution 227
Biometrical methods 9, 208
Biometrical study of crossing over **205**–250
Birds, no crossing over in 200
BLAKEMAN, JOHN 230, *247*
Blending inheritance
  Tobacco 316
  Wheat 56, 92
Blending of hereditary factors 368
BLODGETT, F. H. 152, *182*
Blood color and cocoon color in silkworms **395**–416
Blue roan color in horses and cattle 262
Bombyx mori (see also silkworms) 236, **395**–414

BONHOTE, J. L. 189, 190, 191, *201*, 589, *596*
BOOTH, N. O. 467, *483*
BOTTOMLEY, W. B. 180, *182*
BOVERI, TH. 234, *247*
BRACQUEMOND, FELIX 591
Branching habit in tobacco **307**
BREGGER, T. 265, *274*
BRIDGES, C. B. 194, *201*, 235, 239, 240, *247*, *249*, 275, 276, 278, 279, *282*, **283**, 305, 464, *483*, 509, 519, 527, *533*
BROWN, T. W. 214, *248*
BRYAN, W. E. 2
Bryophyllum 459
Buckwheat (see also Fagopyrum) **534**–586
  Abnormal flowers **538**–540
    Effect of nutrition 542
    Effect of starvation on production of 576, 580
    Effect of temperature and humidity 580
    Position on plant **560**, 564, 565
    Time of production 566
  Abnormal fruits 536, 583
    Supernumerary carpels 538
  Abnormality, factors favoring 584
  Carpel number, variability in 536, 537, 539, 544
  Dimorphic heterostyly 538
  Eversporting variety, periodicity in **558**
  Fasciation **568**–574, 584
    Artificially evoked 573, 574
    Effect of nutrition on 568
    Transmission of 571, 573
  Floral prolification 584
  Flower-yielding capacity 563
  Homostyled flowers 538
  Morphology of flowers 537–542
  Morphology of fruit 537
  Perigone 536–541, 543–547, 554–557, 566, 583, 584
  Periodicity in the occurrence of abnormalities **558**
  Relation of position of buds to time of flowering 567
  Synanthy 542, 584
  Syncarpy 541, 548, 584
  Teratological development **574**, 584
Canary (Fringilla) 200
Cardamine pratensis 475
CASTLE, W. E. 7, *93*, *274*, 346, 347, *355*
Catacorolla 324
Catalyser 352
Cavia (see guinea-pig)
Cell divisions 235
Cell division in Magnolia 483
Cell membranes 353
Chance 257–259
Chance mating 355
Chance segregation of genes 348, 355
Changes in the constitution of germ-plasm (see also mutation) 147
Changes in unit factors 7
Chemotaxis in pollen tubes 472
Cherries (*Prunus cerasus*) 418, 477, 484
  Bing 461
  Double-flowering 462
  English Morello 461, 465, 486
  S. Bigarreau 461, 462
Chevrier beans (Phaseolus) 5
Chicory (Cichorium) 472, 476
Chlorophyll inheritance in maize 392
Choke-cherry (*Prunus virginiana*) 484
Chromatin 147, 274, 346, 347, 423, 430, 431, 434, 436, 482, 507
Chromidia 97, 147
Chromogen 262
Chromosomal combinations 513
Chromosomal complex 508
Chromosome
  Mutation in entire region **275**
  Reduction 474, 479
  Third chromosome of *Drosophila melanogaster* 205
Chromosome map 208
Cichorium 472, 476
Clonal lines **151**, 158, **159**, 160, 164, 170
Clonal selection **151**, **159**, 164, **174**, 181, 182
Clonal variation **151**, 152, **164**, **169**
Clones
  Arcella 95–150
  Lemna **159**–182
CLOS 530, 585
Close-pollination 8, 11
COBEY, W. W. 309, 332, *340*
Cocoon color and blood color in silkworms **395**
Coefficients of association 235, 272, 273
Coefficients of correlation
  Arcella 102
  Drosophila 224, 226, 230, 231, 234
  Tobacco 332, 333
Coefficients of variability 13, 214, 317, 320, 325, 326
COLE, L. J. **183**, 184, 186, 187, 189, 191, 192, 194, 196, *201*, 307, 603, *606*
COLLINS, G. N. 371, *393*
Color
  Correlation 395
  Dilution 262
  Factor, sex-linked **183**
  Inheritance in maize **261**
  Of blood in silkworms **395**–415
  Patterns 261
Combination of
  Characters 339
  Factors **221**, 222
  Genes 509
Compatibility 348, **352**, 353, 360, 363
COMPTON, R. H. 341, 342, *345*, 475, *483*
Constitution of germ-plasm changed during vegetative reproduction 146, 147
Contamination of genes 7, 365, 392, 393
Continuous variables 232
Continuous variation 334, 379
Contractile vacuoles 96, 97
Contrasting colors 188
Coördinates 490

Corn (see also maize) (*Zea mays*) 3, 372
Selection in 367, 368
Correlation between
Aleurone color and endosperm texture in maize 268–270, 272, 273
Average height and coefficient of variation in wheat hybrids 55, 56
Carpels and perigone in buckwheat 557
Chromosome segments in Drosophila 210, 220–226, 228–231, 233, 234, 241
Down and intensity in pigeons 185
Heights of parent and of offspring in wheat hybrids 37, 39, 40, 44, 48, 50
Leaf characters and branching habit in tobacco 309, 338, 339
Parental leaf width and leaf width of offspring in wheat 60, 63, 73, 79, 84, 86, 87
Twins 489–491, 493, 495–497
Weight of suckers and number of suckers in tobacco 325, 330, 332
CORRENS, C. 364, 475, *483*
Coupling (see also linkage) 7, 199, 235, 237, 270, 272, 274
Criss-cross inheritance 285
CROCKER, WM. 417
Cross-fertility 343, 356
Cross-incompatibility 475, 476
Crossing over **205, 209, 211, 218, 219, 227**
Biometrical study of **205**–250
Drosophila 225–241, 289, 291, 294–296, 300, 303, 305, 507–509
Effect of food and season **218**
Mechanism **205, 209,** 210, 216, 218, 220, 221, 223, 225, 227, 228, 239, 240
Modifiers of 218, **219,** 222
None in female birds 200
Pigeons 198–200
Problem 205, 209
Ratio (see also crossover values) 211, 213, 217, 218, 221–223, 226, 227, 234, 239–241, 286
Theories 205, **209,** 210, 216, 227, 233–240, 247, 507
Variations 205, **211**
Crossover values
Drosophila
Curled-spineless 213
Dichaete-curled 213
Dichaete-hairless 301
Dichaete-rough 213
Dichaete-spineless 211, 213
Dichaete-sooty 213
Dichaete-vortex III 290
Hairless-sooty 213
Sepia-curled 208
Sepia-dichaete 208, 211, 213, 285
Sepia-hairless 208
Sepia-peach 208
Sepia-rough 208, 213
Sepia-sooty 208, 213
Sepia-spineless 208, 213
Sooty-rough 211, 213
Spineless-hairless 213
Spineless-sooty 211, 213
Crossover values (continued)
Drosophila (continued)
Star-dichaete 305
Star-flipper 305
Star-morula 525
Star-streak 296, 299
Star-vortex II 289, 296, 299
Vortex-flipper 305
Yellow-abnormal abdomen 276
Yellow-broad wings 277
Yellow-cleft 529
Yellow-echinus 277
Yellow-eosin 276
Yellow-facet 276
Yellow-fused 502
Yellow-notch 276
Yellow-rudimentary 515
Yellow-white 276
Maize
Aleurone color-spotting 270
Pigeons
Intensity-modifier of black 199
Crossover values are correlated variates 225, 226, 236, 241
Cross-pollination 349, 419, 450
Cross-sterility 355, **356,** 361, 433, 442, 471, 472, 478, 481
CUÉNOT, L. 346, *355, 415*
Cultural methods (see technique) 97, 563
Cultures
Drosophila 207, 289, 300, 304, 305
Lemna 160, 162, 164
CURTIS, MAYNIE R. 182, 214, *248*
Curves of distribution 62, 206, 491, 493, 544
Carpel number in buckwheat 544
Shape in Lemna 163
Size in Lemna 157
Size relations in twins 491, 493
Spine number in Arcella 104, 106
Cytoplasm and nucleus, relations between 139
DANFORTH, C. H. **587,** 594, *596*
DARWIN, C. 185, *201*
DAVENPORT, C. B. 498, *499,* 587, 590–592, *596*
DAVIS, B. M. 467, 472, *483*
Decreased size, inheritance of **173**
Decrease in variability 77, 87
Deficiency-allelomorph compound 278
Deficiency in Drosophila 275–280, 289
Deficiency of tortoises in guinea-pigs 598, 604
Deficient region 277, 281
DESLONGSCHAMPS 539
Determination of sex 346
By spermatozoa 498, 499
Man 498
White fly **251,** 256, 257, 260
Determiners (see also genes) 346, 349, **364,** 566
DE VRIES, H. ix, x, frontispiece, 364, **415,** 535, 545, 547, 554, 558, 559, 565, 567, 568, 573, 574, 575, *585*
Diatoms 97
Dibro, Drosophila 502, **527,** 528

Differential mortality in white fly 260
Differential rate of division (see reduplication) 209
Differential viability 221, 222, 603
Difflugia corona 97, 114, 122, 147, 148
DIGBY, L. *483*
Dimorphism 534, 535, 538, 554, 571, 573
Dioeciousness, effects on sterility 467
Dipsacus sylvestris torsus 535, 574
Disturbing factors 214, 215, 217
Division of mother-cells in hybrids 436
Dominance 58, 264, 382, 496, 497
  Imperfect dominance 58, 276, 303
Dominant factor and sterility in Drosophila 505
Dominant genes lethal 281
Dominant inhibitors in wheat 76, in maize 272
Dominant modifer 300, 306
Dominant red in pigeons **186**, 188, 191, 200, 202
DORSEY, ERNEST 417
DORSEY, M. J. **417**, 418, 426, 433, 443, 453, 467, *483*
Double crossing-over 206, 207, 211–217, 225–236, 239–241, 298
Double recessive 200
Doubleness 439
Dove (Columbidae) 200
DRINKARD, A. W. 422, *483*
Drosophila ampelophila 501, 533
Drosophila melanogaster 501
  Abnormal abdomen 276–279
  Acrostical hairs 281
  Australian wild stock 526, 529
  Bar-deficiency 276, 279, 280
  Bar eyes 504–510, 515–528
  Bigenic nature of the vortex character 283, **285**, 286, 287, 306
  Biometrical study of crossing over **205**
  Blood 277
  Body color
    Sepia 207–209, 211, 213, 220–227, 237 277, 285
    Sooty 207–227
    Streak 283, 296–300, 306
    Yellow 529
  Body size
    Dwarf 502, **527**–532
  Bristle character
    Dibro 502, **527**, 532
    Dichaete 207–209, 215–217, 220–227, 237, 238, 283–**290**–**292**–295, 299, 301, 305, 306, 527
  Bristle number 221
  Bristle reduction
    Hairless 207–209, 216, 217, 225, 301, 302
    Morula 5
    Reduced 502, 524, **526**, 527, 530, 532
    Spineless 207–227, 237
  Bristle selection 6
  California wild stock 283, 526, 529
  Culture conditions, effect of 279
  Deficiency-allelomorph compound 278
Drosophila melanogaster (continued)
  Dibro 502, **527**, 532
  Dichaete 207–209, 215–217, 220–227, 237, 238, 283–**290**–**292**–295, 299, 305, 306, 527
  Egg-laying capacity 526
  Exceptional females 520, 521
  Exceptional males 510, 512, 515, 521
  Eye color
    Blood 277
    Cherry 277–279
    Coral 277
    Crimson 275, 525, 526, 528
    Garnet 277
    Eosin 275–277, 280, 281, 503, 510, 525–528
    Maroon 529
    Peach 207, 208
    Pink 277
    Purple 275
    Red 275, 503, 505, 510, 525
    Vermilion 277
    White 276–278, 280, 282, 503, 510
  Eye shape, facet arrangement, etc.
    Bar 504–510, 515–528
    Echinus 277, 282
    Facet 276–282
    Kidney 217, 220, 223, 225, 227
    Morula 502, 524, 525, 528, 530, 532
    Rough 207–213, 217, 220–227, 527
    Star 283, 285, 286, **292**, 294–297, 299, 305
  Fertility of fused female 503, 506, 509, 521
  Infertility of fused stock 503–506
  Interference of streak and vortex 298, 299
  Intergrades in vortex character 285
  Lethal factors 279, 281, 354, 512
  Linearity of regression 228–230
  Microchaetae 283, 284
  Modifiers for crossing over 218, **219**
  Modifier for morula 525
  Modifying action of rudimentary on sterility 522
  Mutation **275**–282, 304, 507, 522
  Non-virginity errors 207, 304
  Not-sterile factor 508, 509
  Parent and offspring correlations 220, 221, 241
  Production of but one sex by fused females 509
  Quadruple crossovers 215
  Ratio of crossing over (see also crossover values) 211, 213, 217, 218, 221–223, 226, 227, 234, 235, 239–241, 286
  Ratio of twist in chromosome 210, 213, 233
  Recessive in the Y chrosome 532
  Scutellar bristles, extra 281
  Season, variations of 218, 241
  Second chromosome 214, 286, 289, 292, 293, 298, 304–306, 526
  Selection experiments 219, 223, 241, 300
  Sterility gene 506–508, 514, 521, 525–532

Drosophila melanogaster (continued)
Sterility in fused stock 502
Sterility in males 279
Sterility, intra-specific **501**–533
Sterility of mutants 530
Streak vortex modifier **300**
Third chromosome **205, 211,** 207, 213, 214, 226, 233, 277, 290–294, 301, 304, 305
Variations in crossing-over 205, **211, 214**
Veins 280
Viability 205, 221, 222, 520, 526
Vortex **283, 284, 285–288–292, 296, 300, 301, 302**–306
Vortex intensifier 283, **302**–305
Wing character
Beaded 391, 537
Cleft 502, 528–532
Club 304
Curled 225
Flipper 283, **304,** 305
Fused **502,** 503, 508–517, 520, 521, 525, 529–532
Miniature 516
Notch 275–282
Notch deficiency 275–282
Rudimentary 502, 513, 516, 517, 519–524, 531
Duck (Anas) 3, 4
Duckweed (see Lemna) 151–182
Duplication 289
Dwarfs 304, 335, 337, 502, 528, 530, 532
EAST, E. M. 2, 4, *93,* 262, *274,* 308, 309, 310, 334, 335, 339–**341,** 344, 345, **346,** 349,, 352, 354, 355, **356,** 365–366, 367, 382, *393,* 464, 467, 472, 473, 476, 477, *483,* 531, *533,* 575, 576, *585*
EICHLER, A. W. *585*
Embryology, experimental 595
EMERSON, R. A. 261, 270, 274, 310, 335, 339, *340,* 374, 391, *393,* 414, *415*
Endocrine gland 595
Endosperm 3, 4, 263, 274, **364, 372,** 444, 453, 456, 457, 479, 488
Enforced heterozygosity 376
Environment 100, 112, 144, 146, 182, 206 207, **218,** 222, 241, 307–309, 314, 338, 340, 347, 356, 418, 426, 497, 543, 557, 565, 573 574, 584
Agencies 573, 575
Characters dependent upon for realization 581
Factors 104, 131, 144, 148, 301, 316, 566, 581
Influence 12, 37, 46, 63, 128, 143, 145, 307, 376, 550, 566, **574**
Enzymes 262, 353, 427
Ever-sporting varieties 535, 538, 547, 549, 553, 554, 558, 560, 571, 574, 583, 584
Evolution 146, 147, 150, 483
EWERT, R. 458, *483*
Extension factors 597
Extra sex chromosome 502, 510, 520
Fagopyrum esculentum 538–540, 573
Fagopyrum tataricum Gaertn. (see also buckwheat) **534,** 535, 537–542, 558, **568**–570, 578, 579, 581, 583
FARR, C. H. 427, *483*
Fasciation 324, 573
Fertility (see also pseudo-fertility) 30, 359, 360, 475, 525, 526, 529
Fertilization
Drosophila 515, 518–521, 532
Plum 418, 438, 443–445, 450, 452, 453, 456, 457, 462, 463, 467, 470, 476, 481, 486, 488, 499
Tobacco **346,** 352, 355
Fertilization, selective **346**
Fertilized eggs, sex of 251, 252, 259, 260
FISHER, R. A. **489,** 496, *499*
Fixing of type 309
Flowering time of peas and rice 7
Fluctuation 75, 205, 240, 290, 291, 309, **332,** 386, 589
Food 207, 218, 219, 222, 241
Formulae
Coefficient of correlation 223, 230
Coefficient of variability 88
Deviation from regression line 230
Measure of resemblance 490
Probability 257
Probable errors 230, 397
Ratio between chromosome twists 234
Fowl (Gallus) 587–596
Aberrant cases 589
Ancestry 588
Barred Plymouth Rock 588
Basal phalanx 592
Black Minorca 588, 589, 592
Booting 587, 590, 596
Brachydactyly 587–596
Brahma 588, 590, 595
Cartilages 593
Cochin 595
Dark Brahma 595
Dorsum 591, 592
Down 587
Effect of alcohol 588
Feather-germ 594
Feathering 594–596
Foot 595
Hamburg 589
Hereditary complex **587**
Langshan 589, 595
Leg-feathering 587, 595, 596
Minorca 589
No crossing over in the female 200
Non-ptilopod 595
Phalanges 593
Ptilopody 587–596
Scale-forming tissues 592
Scales of foot 591, 592, 594
Scutella 587, 591, 594
Secretion of endocrine gland 595
Silky 589, 595, 596
Skeleton 594
Somatic combinations 589
Syndactyly 587, 590, 593, 595, 596

Fowl (Gallus) (continued)
Tarsus 587, 589, 591, 592, 596
Toes 587, 589, 591, 593, 596
Yokohama 589, 596
Fragaria 426, 428, 429, 433, 436
FREEMAN, GEO. F. 1
Frequency distributions
Arcella 104, 106
Buckwheat 545, 546, 562, 563, 584
Drosophila **211**, 213, 247
Lemna 157, 158, 160–178
Tobacco 315, 316, 320, 324, 326, 331, 336
Twins 490
Frequency surface 490
Frogs 498
FRUWIRTH, C. 4, 5, 6, *93*
Gametic coupling (see linkage) 2, 7
Gametic selection 2
Gametophyte 440, 442, 473, 474
GARDNER, V. R. 418, 460, 472, *483*
GARNER, W. W. 307
GATES, R. R. 235, *248*, 464, *483*
GAVIN, W. 214, *248*
GEERTS, J. M. 235, *248*
Generative cell of pollen 431, 478, 482
Genes
Duplication of 289
Homologous 348, 591
Modifying 591
Multiple 2, 270, 334, 339
Nature of 216, 347
Plural 413
Germinal variation 310, 317, 324
Germination percent 457
Germ-plasm 128, 146, 147, 347, 418, 442, 463, 502, 592
GODLEWSKI, E. 235, *248*
GOEBEL, K. 574, *585*
GOFF, E. S. 418, 419, 446, 448, 472, *483*, *485*
GOLDSCHMIDT, R. 209, *248*
GOODALE, H. D. 198, 200, *201*, *248*
GOWEN, J. W. **205**
Grape (Vitis) 427, 428, 459, 467, 469, 482
GRAY, A. 152, *182*
GRAY, JAMES 417
Green stigma in Primula 237
GREENWOOD, M. 214, *248*
GREGORY, R. P. 235, 237, *248*, *415*
Growth adjustments in Bryophyllum 459
Guinea-pigs (Cavia) 261, **597**–606
Chocolate pigment 597, 599–602, 605
Deficiency of tortoises 598, 604
Dilution factors 261
Excess of self-blacks 604
Excess of tortoises 598, 604
Litter size 603, 604
Self-black 598–605
Self-red 598–606
Tortoise 598–606
Triple allelomorphic series **597**, 598
GUPPY, H. B. 163, *182*
HALSTED, B. D. 372, 373, *393*
HARRIS, J. A. 545, *585*
HASSELBRING H. 311, *340*
HAYES, H. K. 3, *93*, *262*, 274, 308, 309, 311, 334, 339, *340*, 365–367, 382, *393*, 575, 576, *585*
HEDRICK, U. P. 419, 421, *485*
HEGNER, R. W. **95**, 142, *150*
HEIDEMAN, C. W. 418, 420, 446, 466–469, *485*
Height, wheat 11, **31–52**–57, 84
HEINICKE, ARTHUR I. 458, 469, *485*
HERBST, C. 235, *248*
HERIBERT-NILSSON, N. 559, *585*
HERON, DAVID 235, *248*, *249*
HERTWIG, R. 498, *499*
Heterosis 53, 58, 92, 310, 317, 330, 334, 338
Heterotypic division **424**
Heterozygosity 11, 12, 20, 30, 53, 55–57, 76, 91, 92, 330, 338, 376, 414
Heterozygous female 207, 209, 222, 223
Hibiscus ocidiroseus 335
HOGE, MILDRED A. 581, *585*
Homozygosis 351, 362, 363, 374, 414
Homozygosity 11, 16, 24, 28, 62, 376, 508
Honey bee (Apis) 252, 260
Hooded rats 7
Hormones 473
HOSHINO, YUZO 7, *93*
Humidity and temperature as factors in floral abnormalities 580
HURST, C. C. 587, *596*
Hybridization 2, 396, 476
Hybrids
Chinese maize **261**, 263, 264, 266, 267, 269, 270, 274
Plum 421, 425, 435, 436, 437, 440, 442, 463, 478, 479, 486
Silkworms 397, 398
Wheat 11, 13, 14, 16, 18, 22, 23, 28–32, 34, 37, 40–45, 48, 49, 53, 55, 58, 69, 73, 77, 78, 83, 84, 87, 88, 92
HYDE, R. R. 502, *533*
IBSEN, H. L. **597**, 605, *606*
IKENO, S. *415*
Imperfect dominance 58
Inactivation 276, 280
Inbreeding 221, 380, 501, 508, 530
Incompatibility 348, 352, 353, 361, 472, 481
Causes of 476
Incompatible cross-pollinations 348
Incompatible pollen-tubes **352**, 353
Incomplete dominance 264
Incomplete segregation 365, 368
Incomplete viability 604
Inconstancy of genotype 96
Increased size, inheritance of in Lemna **174**
Independent segregation 364
India wheat (Fagopyrum) 535
Infertility 357–359, 525
Infinite population 257, 258
Inhibitors 3, 76, 575
Integuments of plum 438, 443, 449, 488
Interindividual variation 206
Intra-specific sterility **501**, 532
Intra-sterile classes 363, 476

ISHIKAWA, C. 396
JANSSENS, F. A. 239, *248*
JENNINGS, H. S. 95–98, 102, 114, 122, 147, *150*
JOHANNSEN, W. 4, 5, 6, 147, *150*, 151, 181, *415*
JOHNSON, JAMES **307**
JONES, D. F. 2, **364**
JOST, L. 472, 473, *485*
JUEL, H. O. 436, *485*
KAGOYAMA, T. 396
KELLEY, FRANK J. **183**
KELLOGG, V. L. *415*
KEMPTON, J. H. **261**, 265, *274*, 371
KIRKPATRICK, W. F. 194, 196, *201*
KNIGHT, L. I. 417, 432, 453, 472, *485*
KÖLREUTER, J. G. 343
KRAUS, F. J. 469, 472, *485*
LANCEFIELD, D. E. 522, *533*
Latency 413, 415
LAXTON BROTHERS 376
LEHMANN, ERNST 560, 585
LEIDY, J. 97, *150*
Lemna minor **150**–182
  Aberrant shapes in fronds 164
  Acquired size, inheritance of 172, **173**, 182
  Apical region 152
  Asexual propagation 165, 181
  Bimodal condition 158
  Budding, mode of 152, 154, 181
  Budding, speed of 154, 165, 169, 181
  Buds 152, 154, 156, 173
  Diverse strains 158
  Effect of culture media 159–161, 171–173, 181
  Frequency of shape types 161
  Fronds in wild population 153, 154
  Leaves 152
  Permanency of size races 158
  Physiological variations 181
  Races in wild population 154
  Shape of frond **152–159–161–164**, 181
  Size of frond **169–172–173–174**–181
  Stem 152
  Variation
    And selection in shape of frond **159**, 181
    And selection within clonal lines **151**, **159**
    In root growth **156**
    In size 157, 158, 181
    In speed of propagation 156, 164–167, 181
    In a wild population 152, 154
Lemna polyrrhiza 152
Lens esculenta 4, 6
Lepidoptera 198
Lethal factor 2, 195, 198, 201, 275, 276, 279, 281, 289, 354, 376, 483
LEVINE, M. 436, *485*
Lily (Lilium) 426
LINDSTROM, E. W. 392, *393*
Line stuffs 475
Linkage (see also coupling, repulsion) 3, **183**, 198, 201, 235–237, 270, 274, 286, 289, 290, **292**, 295, 304, 589
LITTLE, C. C. *415*, 597, *606*
LLOYD-JONES, O. 184, *201*
LOCK, R. H. 316, *340*, 364
LOEB, J. 459, *485*
LOISELEUR 539
Long style, Primula 237
LORD, O. M. 446, 448, *485*
LOVE, H. H. 182
Lupine (Lupinus) 6
LUTZ, A. M. 235, *248*
LYNCH, CLARA **501**
LYNCH, VERNON 114
MACDONELL, W. R. *214*, *248*
MACDOWELL, E. C. 3, 6, 93, 220, *248*, 392, *393*
Maize (*Zea Mays*) **261**, 263, 270, **364**, 365, 389, 391, 414
  Aleurone 262, 267–**270**, 274, 392
  Algerian variety 262–264, 269
  All-colored ear 267, 273
  Anomalous endosperm **372**, 374
  Back-crosses 375, 382
  Basic factors 264, 265
  Black 261
  Blue 262–264
  Brown 261
  Chemical composition 366, 371, 382, 392
  Chinese maize, hybrids of **261**
  Chinese waxy type 261–264, 269
  Clay aleurone color 261
  Comparative effects of double female endosperm nucleus and second male nucleus 382
  Corneous-floury endosperm 382, 383
  Cytological aberrations 374
  Dilution factors 261, 274
  Endosperm 364–366, 369, 370, 382, 386, 391
    Chemical composition of 392
    Deficiencies 366
    Development 383, 385, 388–390
    Factors 376, 377, 383–385, 387, 393
    Texture 263, 265, 268, 269, 274
  Flint corn 366, 374
  Floury corn 366
  Floury starch 370
  High-protein strain 365
  Horny endosperm 263
  Mottled seeds 261
  Pale color 261
  Physiological correlation 386
  Pink 261
  Plant factors 373, 383, 384, 385, 393
  Popcorn 366
  Pseudo-starchy endosperm 364, 367, 369–371, **374**, 375, 382–384, 386, 387, 390
  Purple seeds 261–263
  Red seeds 261–264
  Selection of pseudo-starchy endosperm **364**

Maize (*Zea Mays*) (continued)
Semi-flinty corn 373
Semi-starchy endosperm 364–366, 368, 382, 391
Somatic mutations 374
Spotted aleurone color **261**
Spotted seeds 262, 264–266, 269–274
Spotting factor 268, **270**, 271, 274
Starch grains 366, 369, 371
Starchy seed 364–367, 382, 389, 391, 392
Sweet corn 364–366, 373, 375, 384, 386, 389, 391
Waxy endosperm 366, 371
White seeds 264–268, 270, 273, 274
Male 207, 236, 253, 254, 257–260
Crossing over in 201
Gamete 269, 498
Male gametophyte 355
Males, percentage of 258
Marital correlation 497
Mass selection 6
Mathematical universe for double crossing over 228, 232
Matthiola (see also stocks) 535, 574
MAUDE, L. C. 409, *415*
MCCLUNG, C. E. *248*
Mechanism of heredity 234
MENDEL, G. 2, 346, 364, 395, *415*
MENDIOLA, N. B. **151**, 170
Methods (see technique)
METZ, C. W. 276, *282*
Mice
Lethal factors 354
Yellow body color 281, 346, 603
MIDDLETON, A. R. 96, 147, *150*
Migonette (Reseda) 341
MILES, F. C. *415*
Mirabilis Jalapa 343, 344
Mirabilis longiflora 343, 344
Modification, non-heritable 535
Modification of genetic factor 414
Modifying factors 205, **219**, 221, 222, 241, 261, 299, 301, 303, 304, 306, 591
MOHR, OTTO L. **276**, **283**
MOORE, C. W. 432, *485*
MORGAN, T. H. 234, 239, 240, *248*, *249*, 275, 278, 279, *282*, 304, 347 392, *393*, 464, *485*, 513, 516, 532, *533*, *585*
MULLER, H. J. 214, 239, *249*, 281, 376, 391, *393*, 531, *533*
MÜLLER-THURGAU 458, 485
Multiple allelomorphism 345, 597
Multiple factors 2, 270, 334, 339
Mustard (*Sinapis alba*) 6
Mutation
Arcella **127**, 131, 146, 148
Drosophila **275**, 282, 285, 507, 521, **522**, 523, 527, 528, 532, 533
Fowl 591
Guinea-pig 605
Lemna 164, 182
Not visible in the first generation 146
Of an entire region of chromosome **275**
MYERS, C. H. 182
Natural selection 181
Nicotiana (see tobacco) 4, **342**, 467, 472, 477
Self-sterility 345, 531
Nicotiana alata 4, 342, 343, 345, 348
Nicotiana angustifolia 345, 348
Nicotiana Forgetiana 342, 345, 348
Nicotiana Forgetiana × *alata* 349–351, 356
Nicotiana Forgetiana × *Langsdorffii* 342, 343, 345
Nicotiana glutinosa 345
Nicotiana Langsdorffii 4, 342, 343
Nicotiana Langsdorffii × *alata* 343–345
Nicotiana longiflora 4
NILSSON-EHLE, H. 3, 7, *93*, 334, *340*, *415*
Non-disjunction 194, 278, 280, 509, 512, 521, 532
Non-extension factor 605
Non-Mendelian inheritance 7
Non-viability of a class of zygotes 603
NORTON, J. B. 310, *340*
Nuclear reorganization 436
Nucleolus 431, 436, 482
Nucleus 4, 97, 139, 142, 147, 274, 382, 423, 428–431, 435, 436, 443, 478, 479, 481, 484
Nucleus and cytoplasm, relation between 139
NUTTALL, J. S. W. 190, 191, *201*
Obturator 444
Oenothera 348, 467, 472, 559, 574
Embryo abortion 472
Fasciation 574
Non-viable seeds 467
Selective elimination 348
Oenothera Lamarckiana 559
OSTERWALDER, A. 432, *485*
Paramecium 180
Parents and offspring, correlation 108, 113, 115, 121, 125
PARK, J. B. 341, 344, *345*, 349, 352, *355*, 356, 359, 472, 473, 476, 477, *483*, 531, *533*
PARSHLEY, H. M. 498, *499*
Partial extension 597, 603
Partial inhibitor 274
Partial viability 603
Patency 413
Paternal correlation 496, 497
PAYNE, F. 392, *393*
PEA (Pisum) 7
Pear (*Pyrus communis*) 487
PEARL, R. 214, 240, *249*, 370, 392, *393*, 498, *499*, 502, 533
PEARSON, KARL 217, 223, 230, 232, 235, *249*
PÉCHOUTRE, F. 443–445, 453, 464, *485*
PENZIG, O. *585*
Pepper (Capsicum) 335
Permanent variations produced by selection 309
PERTZ, D. F. M. 554, *585*
Petalody **437**
PETERS, REG. W. 418, 446, 452, *485*
PEYRITCH 574
Phaseolus vulgaris (see also bean) 5
Pheasant 4

Phenotype in disagreement with genotype 573, 597–603
PHILLIPS, J. C. 3, 4, *93*
Phyllotaxy 568, 571
Physiological characters highly variable 214, 240
Physiological weakness in tobacco 337, 339
Picris hieracioides 574
PIETERS, A. J. 471, *485*
Pigeons 183–203
  Absence of crossing over in female 199–201
  Baldhead pattern 189
  Barred types 188
  Colors in domestic 184, 202, 203
  Descriptions of colors **202**
  Down and intensity, correlation between 185
  Eye-color 184
  Fantail 189, 190
  Gray, dominant **186**, 200, 202
  Intensity **184**–186, 189, 192, 194, 195, 198, 200
  Pigment modifiers 184
  Red-barred 188
  Red, dominant **186**, 200, 202
  Sex-linked character **183**, 198, 200
  Tumbler breed 186, 189
Pistil abortion **446**, 447
Pistillody **437**
Pisum arvense 5
PLOUGH, H. H. 239, *249*
Plum **417**–488
  Aborted pistil **446**, 447, 448
  Aborted pollen 425, 426, 432, **433**, **435**–437, 439, 440, 442, 462, 463, 479, 481
  Abscission 438, 439, 443, 444, 452, 455, 467, 471, 488
  Acalycine flowers 437
  Anther suppression 438
  Antipodals 479
  Archesporial cell 422, 423, 477
  Arrested development 481
  Calyx 438, 439, 447, 449, 455, 480
  Carpel 438, 443, 444
  Chalaza 443, 444, 449, 452, 479, 484
  Cotyledons 457, 482
  Curculio strings 455–458
  Cytoplasm 426–436, 444, 482
  Cytoplasmic abortion 433
  Dehiscence of anthers 418, 442, 478
  Diakinesis 424, 436
  Dioeciousness 449, 467, 469
  Double-flowered 439
  Dropping of pistils **446**, 447, 479, 481
    First drop **446**
    Second drop **449**
    Third (or June) drop **454**, **456**, **458**, 471, 479
  Elimination of gametes 462–464
  Embryo abortion 445
  Embryonic development 462, 479
  Embryo-sac 438, 443, 444, 445, 452, 453, 458, 464, 473, 479, 481, 484, 488
  Enzymatic process 442
Plum (continued)
  Epidermal layer 422
  Epidermis 443, 444
  Exine 430, 433, 437
  Flowers 467, 468
  Fruit development dependent on seed development 469
  Genetic relationship **465**, 466, 470
  Germ-cell formation 475
  Germination of pollen in artificial media 472
  Germination tests 472
  Germ-pore 429, 431, 433, 434, 478, 482
  Gynaecium 473
  Heterotypic division 424–428, 435, 436, 463, 478
  Homeotypic division 425
  Interspecific combinations 465, 466
  Intersterility 420
  Intine 431
  Megaspore mother cell 479
  Microspore (see also pollen) 425–429, 433, 436, 440, 463, 474, 478, 481, 482
  Microspore nucleus 430, 434
  Microspore wall **428**, 482
  Middle lamella 427, 428, 444
  Mother cells 423, 427, 428, 434, 436, 478, 479
  Mother-cell wall 426, 427, 478, 482
  Multipolar spindle 424
  Non-pollination 458
  Nucellus 438, 443, 444, 457, 482, 484, 488
  Ovule 443–445, 448, 452, 458, 463, 471, 478–482, 486, 488
    Suppression of one **445**, 448, 452, 464, 478–482, 486, 488
  Pedicel 449, 455
  Petalody **437**, 438, 486
  Petaloids 438
  Petals 438, 478, 486
  Pistil 419, 421, **442**, **443**, 446–452, 457, 460, 462–464, 467–470, 473, 478–482, 488
  Pistil development **442**, 478
  Pistil suppression 469
  Pistillody **437**, 438, 486
  Pistilloids 438
  Pit 445
  Placenta 444
  Plasma membrane 427, 428
  Pollen **431**, **433**, 435, **436**, 437, 440–442, 457, 462–464, 467, 471, 474
  Pollen abortion 425, 426, 432, **433**, **435**–437, 439, 440, 442, 462, 463, 478, 479, 481
    In hybrids 435, 442
  Pollen degeneration 422, 425, 442
  Pollen development **421**, 422, 439, 477, 478, 479
  Pollen mother-cell 422, 423, 477, 478, 482
  Pollen suppression 463, 479
  Pollen tube **431**
  Pollen viability 472
  Pollenizers 419, 420

Plum (continued)
Reduction divisions 436, 474, 475, 477
Secretions of the egg 473
Sex structures 421
Sexual affinity 466
Single ovule 471
Spindle 424
Spireme 423
Stamen suppression 469
Staminate flower 469
Sterility **417,** 419, 420, 460, **462,** 465, 467, 471, 472, 476, **477,** 478
Stigmatic cells 443, 473
Stigmatic fluid 474, 481
Stylar tissue 431
Suppressed embryo 445, 456
Tapetum 423, **425,** 427, 437
Tetrad 425–428, 433, 436, 463, 482
Tetrad degeneration 482
Tetrad nuclei 427
Tetrad wall **426**–429, 437, 478, 482
Varieties
Abundance 420, 422, 440, 450, 461
Aitkin 441
Assiniboin 420, 450, 451–486, 488
Blush 441
Burbank 420, 422, 440, 441, 450, 455, 460–462, 482, 484, 486
Cheney 441, 488
Chicasaw 447
Compass 420, 441, 454–457, 460–462, 465–467, 484, 486
De Soto 441
Early Red 466
Etopa 420, 441
Hiawatha 446, 466
Iron Clad 425, 431, 441
Kamdesa 484
Loring 441
Manitoba 441, 451, 455, 460–462, 488
Milton 465
Miner 447
Minnesota No. 1 461
Minnesota No. 5 482
Minnesota No. 6 420, 455 461, 462, 465
Minnesota No. 8 420
Minnesota No. 9 461, 462, 465, 466
Minnesota No. 10 420
Minnesota No. 12 420, 425, 460–462, 465, 466
Minnesota No. 17 484
Minnesota No. 18 450
Minnesota No. 21 420, 450, 451, 455, 456, 459, 480, 482, 484, 486, 488
Minnesota No. 35 420, 450, 461, 462, 465, 484, 488
Moreman 446
New Ulm 418
Ocheeda 441
Opata 425, 441, 484
Robinson 418
Rollingstone 441
Sapa 441
Plum (continued)
Satsuma 484
Sophie 465
Stella 425, 446, 456, 486
Stoddard 425
Surprise 420, 422, 425, 441, 461, 462, 486
Terry 461, 462
Wakapa 420, 451
Wayland 447
Whitaker 465
Wickson 448
Wild goose 447, 465
Winnipeg 454, 455
Wohonka 420, 451, 484
Wolf 420, 441, 448, 450, 466, 484
Wyant 425, 429, 431, 441
Yellow egg 420, 431, 441, 452–457, 460–462, 465–467, 486, 488
Pollen grain 354, 355, 430, 474
Germination 348
Pollen-tube **349, 352, 431,** 432, 443, 472, 473, 481
Frequency distributions **349**–352, 354
Growth 348, 349, 351
Nucleus 352
Pollination 73, 349, 352, 357–359, 373, 374, 390, 418, 451, 453, 458, 463, 467, 488
Polygonaceae 539, 540
Polygonum 539, 540
Polygonum orientale 539
Polygonum Persicaria 539
Polygonum pyramidatum 539
Polygonum tataricum (see Fagopyrum and buckwheat) 535, 539
Polygonum tinctorium 539
Popcorn (see maize) 366
Powys, A. O. 214 *249*
Practical breeding 563
Predominance 190
Prematuration 513, 520, 521, 526, 531, 532
Primula 236–238
Probability 257–259
Probability integral 491
Probable error 10, 173, 179, 267, 409, 493
Prunus (see also plum, cherry) 433, 439, 440, 443, 465, 467, 472
Prunus americana 418, 419, 420, 422, 425, 441, 446, 447, 451, 457–459, 462, 465, 466, 480
Prunus americana mollis 419, 422, 425, 440, 441, 484
Prunus americana × *triflora* 425, 486
Prunus angustifolia 441, 482
Prunus armenica 435, 465
Prunus Besseyi 418, 419, 420, 422, 430, 435, 441, 449, 461, 465, 470, 473
Prunus Besseyi × *americana* 441
Prunus Besseyi × *armenica* 441, 482
Prunus Besseyi × *hortulana Mineri* 441
Prunus Besseyi × *Mineri* 441, 465
Prunus Besseyi × (*P. Munsoniana* × *triflora*) 425, 441
Prunus Besseyi × *Simoni* 441, 484

Prunus Besseyi × *triflora* 441
Prunus Besseyi × (*triflora* × *Munsoniana*) 484
Prunus Cerasus (see cherry) 484
Prunus domestica 418, 419, 421, 422, 430, 431, 441, 444, 447, 452, 453, 459, 465, 472, 476
Prunus hortulana 418, 419
Prunus hortulana Mineri 422, 425, 441
Prunus nigra 418, 419, 422, 430, 441, 447, 465, 486
Prunus pennsylvanica 422, 425, 430, 441
Prunus Pissardi 444, 484
Prunus Simoni 462
Prunus spinosa 464
Prunus triflora 418, 419, 422, 439, 440, 441, 446, 457, 459, 465, 484, 486
Prunus triflora × *americana* 441
Prunus triflora × *americana mollis* 425, 440, 484
Prunus (*triflora* × *americana*) × *P. Cerasus* 484
Prunus triflora × (*Besseyi* × *hortulana Mineri*) 484
Prunus virginiana 430, 441, 484, 488
Pseudo-fertility 342–345, 356, 360–363
Pseudo-starchy endosperm in maize **364**–393
PULLMAN, J. A. 539, *586*
PUNNETT, R. C. 3, 93, 209, 235–238, 247, 249, 587, 589, 595, *596*
Pure cultures 49, 62, 69, 77, 78, 83, 87
Pure lines 5, 6, 11, 12, 15, 24, 31, 34. 40, 45, 58, 88
Pure-line selection 4
Pure-line theory 151, 182
Pygopagus parasiticus 588
QUAINTANCE, A. L. 253
Quantitative characters governed by several factors 379
Quantitative characters, heredity of in wheat 1
Random sampling 218, 225, 236, 257, 491, 486
Range of variability 47, 62, 171, 310, 317, 527, 549, 551, 562, 563
Raphanus raphanistrum 574
Rat (Mus) 7
Reciprocal crosses
  Maize 263, 269, 274, 375, 377, 380, 382, 384
  Tobacco 317, 338
  Wheat 2
Recombination 37, 53, 79, 91, 413
Red stigma, Primula 237
Reduplication 209, 247, 249, 250, 272
Reduplication theory 209, 227, 233–239
REEVES, F. S. 467, *485*
Repugnance 513, 516, 533
Repulsion 199
Reseda odorata 341, 475, **483**
Resistance to Thielavia root-rot disease in tobacco 309
Restoration, principle of 517, 521, 526, 531, 532
Reversion 144
Rhizopod 95, 147, 150
Rice (Oryza) 7
RIDGWAY, R. *201*, 202
Ring-dove (Streptopelia) 185, 186
Rodent crosses 7
ROOT, F. M. 96, 147, *150*
Root-rot disease 309, 314
Rosaceae 443, 445
ROSENBERG, O. 436, 464, *485*
ROSENDAHL, C. O. 417
ROUX 234
Sampling 490
Sand cherry 420, 480
SAUNDERS, E. R. *247*, 310, 335, *340*
Secale 472
Secondary factors 7, 356, 362, 363
Second male nucleus 382
Second moment 209, 211
Seed 263, 309, 314, 364, 392, **444**, 445, **456**–458, 467, 469, 488
Seedless grapes 469, *485*
Segregation 261, 317, 379, 410
  Maize **364**, 365, 368, 375–377, 380–382, 391, 393
  Plum 477
  Rice 7
  Silkworm 398, 401, 405, 406, 408, 410
  Tobacco 4, 316, 317, 330, 334, 337, 339
  Wheat 30, 56, 62, 79, 91
Selection **151**, 174, 179–181, 207, 220, 221, 392
  Among sexually reproducing organisms 142, 143
  Arcella 110, 113, 123, 124
  Based on past performance 114, 123, 135, 148
  Beans 4, 5
  Buckwheat 558
  Drosophila 6, 7, 219, 223, 241, 300
  Lemna 151, 182
  Lens esculenta 4, 6
  Maize 364–393
  Oats 6
  Peas 5, 7
  Protozoa 147
  Rats 7
  Rice 7
  Soy beans 6
  Tobacco 308, 309, 339, 355
  Wheat 15, 45
  White mustard 6
Selection of gametes 348
Selection of genes 348, 354
Selective elimination 348
Selective fertilization 260, 349, 350, 352, 354, 355, 603
Self-colored seeds 6, 263, 264, 269, 271–274
Self-fertility **341**, 343, 344, 475
  A simple Mendelian dominant 475
  Two-factor difference between self-fertility and self-sterility 344
Self-fertilization 6, 362, 374, 391, 392, 538
Self-incompatibility (see also self-sterility) **352**, 475, 476

Self-pollination 268–274, 349, 362, 418, 420, 432, 433, 454, 475
Self-sterile plants 341–345, 348, 350, 352, 355, 356, 361
Self-sterility **341–346–356**–363
  Nicotiana 342–345, 348–354, 356–363, 531
  Plum **418**, 420, 433, 442, 462, 469, 471, 472, 474, 476, 478
  Reseda 341
  Tobacco **341**, 343–**346**, 348, **356**, 361
Semi-sterile hybrids 25
Separation of coupled factors (see crossing over) 209
Sex 236, 252, 254, 259, 498
Sex chromosomes 200, 235, 248, 282, 517, 520, 521
Sex determination **251**–260
Sex-differentiating factor 194
Sex-limited characters 276, 285, 292, 303
Sex-linked characters **183**, 191, 194, 234, 235, 527, 529, 531, 604
  Drosophila 527, 529, 531
  Pigeon **183**–203
Sex ratio 193, 196–197, 201, 251–**253**, 254, 257–260
  Drosophila 503
  Guinea-pig 604, 605
  Pigeons 193, 195–197, 201
  White-fly 251–**253**, 254, 259, 260
Sextiles 491, 492
SHAMEL, A. D. 309, 332, *340*
Shape of fruits, variability in 536
Shell-less Protozoa 99
SHEPPARD 209, 211
Short style, Primula 237
SHULL, A. F. **251**, 252, *260*
SHULL, G. H. 3, *93*, 310, 334, *340*, 413, *415*
Sibs, correlation between 496
Sibship 489
Silkworms (Bombyx) 236, **395**, 401, 414
  Artificial methods of hatching eggs 396
  Back-crosses 398, 401, 403, 405, 414
  Blood color **395**, 396, 408
  Cocoon color **395**, 396
  Cocoons 397, 399, 402, 407, 408, 413, 414
  Races
    Jōsai 396
    Onodahime, 396
    Seiyō 396
    Shōkō 396
    Shōzan 396, 413, 414
    Simpaku 396
    Tōbuhime 396
  Silk-gland **408**, 409, 414
  White-blooded 395
  White cocoon 395, 396, 402
  Yellow-blooded 395, 396
  Yellow cocoon 395, 396
Sinapis alba 6
Size, acquired, non-heritable 181, 182
Size inheritance
  Arcella 97, **124, 127**
  Lemna **173, 174**
  Tobacco 308–310, **325**
  Wheat **31–57**–92
Size of litter, guinea-pigs 603, 604
Size variation
  Arcella **102, 127**
  Lemna **158, 172**
Skew curves 68
SMALLEY, F. W. 189, 190, 191, *201*
Soja bean 5, 6
Somatic mutation 374
Spatial arrangement of genes 347, 348
Species crosses 354
  Nicotiana 342, 343
  Plums 420, 422, 430, 440, 441, 446, 457, 465, 467, 483, 484, 486
  Wheat 53
Spontaneous variations (see also mutations) 6
Stable hereditary units 392
Stamen dehiscence 442
Standard deviations, distribution of 20
  Drosophila 209, 211, 213, 230, 240
  Lemna 171, 173
  Wheat 9–14, 16, 18, 20, 23, 24, 27–30, 37, 58
STAPLES-BROWNE, R. 190, 191, 194, *201*
Starvation, effect on habit of Fagopyrum 575, 580, 584
Stature (see also height and size) 497
Sterility (see also self-sterility) **341, 346, 356**, 361
  Drosophila 304, **501**–503, 505–510, 513, 514, 520–525, 527, 529, 531, 532
  Effect of dioeciousness on 467
  Embryo abortion 472
  Impotence 472
  Incompatibility 472, 481
  Intra-specific **501**
  Plum **417**, 419, **421, 442**, 460, **462**, 465, 467, **471**, 472, 475–478, 481
  Velvet beans 355
  Wheat 20, 25
STEVENS, N. M. 234, *249*
Stimulus of heterozygosis (see heterosis) 330, 338
Stocks (Matthiola) 310, 439
STOLL, N. R. **251**–260
STOUT, A. B. 335, *340*, 472–476, *485*, *487*
Strawberry (Fragaria) 426, 428
Streptopelia risoria 185
STRONG, R. M. 185, 194, *201*
Struggle for existence 458
STURTEVANT, A. H. 209, 214, 235, 237, 239, 240, *249*, 371, 392, *393*, 522, 523, 524, 533
STURTEVANT, E. L. *393*
Stylonychia 147
Subsidiary factors 345
Subspecies 4
Suckers 307, 309, 311, 317, 320, 324–326, 330, 332–334, 338, 339
Sunflower (Helianthus) 310
Supernumerary carpels 537, 539, 583
Supernumerary stigmas 559
Suppression factor for variability 55, 56, 88, 91
SURFACE, F. M. 214, *249*

SUTTON, IDA 418, 476, *487*
SUTTON, W. S. 234, *250*
Sweet cherries (*Prunus Cerasus*) 418, 460
Sweet pea (*Lathyrus odoratus*) 235, 236
SWINGLE, L. 2
Synanthy 542, 562, 564, 582, 584
Synapsis 423, 424, 517, 519, 520
Syncarpy in buckwheat 541, 548, 584
TAMMES, TINE 559, 560, *586*
TANAKA, Y. *250*, 385, 409, *415*
Technique
  Comparing F_2 variability with F_3 11
  Computation of constants 209
  Culture
    Arcella **97**
    Buckwheat 574, 575
    Drosophila **206**, 207, 218, 219
    Lemna minor 159–161, 180, 181
    White fly 253
  Cytological technique, plum 421
  Hatching eggs of silkworms 396, 397
  Keeping pedigrees 98, 100
  Measuring and weighing, tobacco 316
  Preservation of specimens, Arcella **101**
  Recording position on plant, buckwheat 561
TEGETMEIER 185
TERRY, R. J. 596
Theories of heredity 489
Thielavia root-rot disease, resistance to 309
THOMAS, N. *248*
THORNDIKE, EDWARD L. 489, 490, 492, 493 *498*
Thrips 252
Thysanoptera 251
TICE, S. C. *533*
Time of flowering 320, 338, 339
  Relation to position of buds 567
TISCHLER, G. 433, 436, 464, *487*
Tobacco (see Nicotiana) **307**–340
  Branching habit **307**, 340
  Breadth-index 333
  Catacorolla 324
  Dwarf 324, 335
  Fasciation 324
  Flower size 349
  Height 311, 312, 316, 336, 339, 349
  Leaf number 308, 310–312, 314, 334, 338, 339
  Leaf shape 308, 310, 333, 338, 339
  Leaf size 308, 310–312, 316, 319, 338, 339, 349
  Little Dutch-Cuban cross 313–315, 317, 319–324, 326–329, 331, 336, 338, 339
  Morphological monstrosity 339
  Mutations 316, 335, 337
  New character 338, 339
  Number of suckers 316, **317**, 320, 324, 325, 330, 332, 333, 338
  Production of non-suckering types 309
  Quantitative characters 307, 339
  Time of flowering 320, 338, 339
  Topping 308
  Weight of suckers **325**, 330–333, 338
Tortoise-shell guinea-pig 598–606
TOYAMA, K. 395, 409, *415*
Transmission of characters 535
Transposition 304
Traumatic stimulation 552, 568, 573
Trialeurodes vaporariorum (see white-fly) 253, 254, 259, 260
Tricolor inheritance 597–606
Trifolium pratense quinquefolium 535, 559
Triple allelomorphic series in guinea-pigs **597**–606
Triticum compactum 7
TROW, A. H. 235, 237, 238, *250*
Twins **489**, 495, 499
  Cephalic index 494
  Fraternal correlation 496, 497
  Genesis **489**, 497, 499
  Gradations of similarity 493
  Head size 494
  Height 494
  Identical 489, 495, 497, 498
  Inheritance of tendency to twinning 498, 499
  Proportion of identical twins 498
  Resemblance 489, 490, 493
  Sex 498
  Variation in a twinship 489
UDA, H. **395**
Unit character 476
Unlike reciprocal hybrids 263
VALLEAU, W. D. 417, 426, 429, 433, 464, 467, 472, *487*
Variable-force hypothesis of crossing over 247
Variability
  Hybrids 11, 15, 38, 45, 58, 77
  Physiological characters 214
  Plant populations 11
  Quantitative characters 88
  Suppressing factor 55–57, 88, 91
Variance in twins 496
Variation
  Buckwheat 536, 537, 539, 544, 551, 557, 585
  Clonal 164, 169, 170
  Constants 214
  Continuous 334, 379
  Distribution 158
  Drosophila 205, 207, 210, **211**, 213, **214**, 220, 222, 240, 241, 247
  Factors affecting 160
  Fowl 591, 592, 596
  Hybrids 69
  Lemna **151**–182
  Maize 261, 368, 374, 377, 379, 385
  Pigeons 187
  Plums 438, 468
  Silkworms 399
  Somatic 163, 164, 181
  Tartary buckwheat **534**–586
  Tobacco 309, 324, 325, 327, 332
  Vetch 6
  Wheat 12, 13, 16, 23–30, 37, 41, 45, 46, 55, 63, 71, 73, 76, 77, 88, 90, 92
Variegated ears of maize 414

Varieties, ever-sporting 535, 547, 554, **558**, 560, 571, 574
Variety crosses
  Maize 375, 376, 381, 388, 392, 393
  Plum 440, 460–462
  Wheat 14, 22, 31, 81
Varying dominance 416
Vegetative reproduction, heredity and variation in **95**
Vegetative vigor in hybrids (see also heterosis) 92
Velvet bean (Stizolobium) 355
Veronica agrestis 535, 560
Veronica Buxbaumii 554
Veronica Tournefortii 560
Viability of the zygote 603
Viable and non-viable seed 467
Vigor 559
  Hybrid (see also heterosis) 53, 58, 92
Vitis 433, 436, 469
Vitis vinifera 469
WAITE, M. B. 418, 419, 469, *487*
WAKLEY, THOMAS 498, *499*
WAUGH, F. A. 418–420, 437, 446, 448, 453, 454, 458, 465, 472, *487*
WEBBER, H. J. 310, *334*, 335, 340, 364, 540 *586*
Webbing 592, 593
WEBER, C. O. 539, 586
Weighted means 230
Weight of suckers in tobacco **325**, 330–333
WEISMANN 234
WELDON, W. F. R. *250*
Wheat
  Coefficient of variation 4, 9, 11–13, 34–92
  Crosses 7, 14, 22, 25, 31, 39, 43, 48, 53, 54, 56, 57, 68, 81
  Environic modifications 12, 46, 50, 63
  Extreme extension of range of variability in crosses 27
  Filiform leaves 73
  Height factors 11, 37, 41, 44
  Heights of hybrids **31**–57, 84
  Heredity of quantitative characters **1**–93
  Hybrid cultures 11–14, 28–34, 40, 41, 45, 48, 49, 55, 58, 69, 73, 83, 84, 87
  Increase in homozygosity 62
  Increased variability 24
  Influence of heterozygosity 57
  Leaf width **57**–92
  Macaroni-bread-wheat crosses 31, 79, 88, 91, 92,
  Mass culture 9
  Measure of variability 13
  Number of factors in leaf width 92
  Nutritional variations of a pure line 68
  Partial blending inheritance 29
Wheat (continued)
  Partial sterility 2, 25
  Physiological interference 7
  Physiological limitation of growth 88
  Progressive increase in homozygosity 62
  Pure variety 88
  Range of variability in hybrids 27
  Ranges of hybrid populations 49
  Recombination producing variability 12
  Reduced vigor in hybrids 53
  Results of crossing 4
  Segregation, continuous 3
  Size factors 7, 13, 92
  Statistical constants 10
  Time of heading **14**–31
  Variability of quantitative characters 88
  Variable pure cultures 69
  Variation behaviors 7
  Variation due to nutrition 60, 68
  Varieties 8, 9
    Algerian macaroni **8, 14, 31, 37, 43, 57, 68**
    Algerian red bread **8, 22, 43, 46, 68, 77, 81**
    Early Baart **8, 22, 46, 81**
    Sonora **8, 14, 31, 37, 57, 77**
WHIPPLE, O. B. 458, *487*
White fly (Trialeurodes) **251**, 253, 260
  American strains 251
  Chromosome number 252
  English strain 251
  Female 256, 258, 259, 260
  Females that mate 251, 252, **255, 256**
  Mating observed **256**
  Methods of culturing **253**
  Offspring of females that mate 251, **255**
  Offspring of virgin females 251, 254, 255
  Parthenogenetic eggs 251, 252, 259, 260
  Phototropism 253
  Sex determination **251**–260
  Sex-ratio in random collections **253**, 254, 258, 259
  Spermatheca 252, 257
  Unfertilized eggs 251, 254, 256, 259
  Wild collections 253
White Leghorn 588
Width of leaf **57**–87–92
WILLIAMS, C. B. 251–254, 259, *260*
WILSON, E. B. 234, 240, *250*
WRIGHT, SEWALL 261, 262, *274*
Y chromosome, structure and formation of 531
Yellow mice 346, 603
YULE, G. UDNEY 235
Zea mays (see also maize) 366, 574
Zea mays amyleasaccharata 371
ZINN, J. 534
Zygotes, non-viability of a class of 603
Zygotic classes (phenotypes) 271, 272

C30